A taxonomic study of the larvae of four thalassinid species (Decapoda, Thalassinidea) from the Gulf of Mexico

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Introduction

Larvae of American mud-shrimps belonging to the superfamily Thalassinidae are poorly known. The complete larval stages of only three species have been described to date: *Upogebia pugettensis* (Dana) by Hart (1937), *Upogebia affinis* (Say) by Sandifer (1973) (family Upogebiidae), both described from plankton collected material, and *Naushonia crangonoides* Kingsley by Goy & Provenzano (1978), the first stage of which was described from plankton material and the remaining ones from laboratory reared specimens.

The recent material of decapod larvae from the Gulf of Mexico collected by the Virgilio Uribe Cruise (August 1972) contains numerous samples of thalassinid larvae from some stations (see Station List deposited in the Crustacea Section, British Museum (Natural History), London). Three species of *Upogebia*, one of which is probably *U. affinis* (Say), have been identified in this material and also a species belonging to the family Laomediidae and tentatively assigned to the genus *Axianassa*. The latter shows strong affinities to some larvae attributed by Menon (1933) to the subfamily Upogebiinae but is considered here as laomediid.

As two families of the Thalassinidea are considered in this Mexican plankton, it is convenient to discuss the representatives of each under separate headings:

A. Description of the larvae of three species of *Upogebia* Leach from the Gulf of Mexico with observations on larvae and adults of *Upogebia* in the collections of the British Museum (Natural History), London.
B. Description of the larvae of a species of the Laomediidae attributed to *Axianassa* from the Gulf of Mexico.
C. The relationship between larvae of the Laomediidae, those of the Upogebiidae and the adults of the Glypheidae.

Materials and methods

Larvae were sorted from plankton samples taken during the Virgilio Uribe Cruise during August 1972; they were preserved in 5% formalin. The size of the larvae given in the descriptions are the carapace length (c.l.) measured from the tip of the rostrum to the posterior border of the carapace in the mid-line, and the total length (t.l.) measured from the tip of the rostrum to the posterior margin of the telson. Drawings were made, using a *camera lucida,* from whole larvae or dissected appendages mounted in a drop of water.

A. Larval stages of three species of *Upogebia*

Three species of larval *Upogebia* can be recognized in the Mexican plankton material. No characters have been found that enabled the separation of the first larval stage which was

Table 1 Comparison of the successive larval stages of *Upogebia* sp. A, *U. affinis* (Say) and *Upogebia* sp. B

	Upogebia sp. A	*U. affinis*	*Upogebia* sp. B
Zoea I	the three species are indistinguishable		
Zoea II			
Total length (mm)	2·35–2·45	2·30–2·55	2·72–2·80
Aesthetascs on antennule	3, all terminal	2, all terminal	4, all terminal
Setae on antennal scale	10–11	11–12	10
Mandible	without palp	without palp	without palp
Setae on basal endite of maxillule	4 + 3	4 + 3	4 + 3
Setae on exopod of maxilla	6–7	7	6
Setae on endopod of 3rd maxilliped	1	2	1–2
Zoea III			
Total length (mm)	2·56–2·90	2·80–3·06	3·29–3·40
Aesthetascs on antennule	3, 1 subterminal	3, 1 subterminal	3, 1 subterminal
Setae on antennal scale	11–12	11–12	13
Mandible	without palp	without palp	without palp
Setae on basal endite of maxillule	4 + 3	4 + 3	4 + 3
Setae on exopod of maxilla	9–10	11–12	10
Setae on endopod of 3rd maxilliped	1	2	1–2
Setae on exopod of uropods	10–11	11–12	11–12
Zoea IV			
Total length (mm)	2·85–3·00	3·00–3·57	3·80–4·00
Aesthetascs on antennule	3, 1 subterminal	3, 1 subterminal	4, 2 subterminal
Setae on antennal scale	12–13	13–14	14–15
Mandible	without palp	with palp	without palp
Setae on basal endite of maxillule	6 + 3	6 + 4 + 1	6 + 3
Setae on exopod of maxilla	10–11	13–14	12–13
Setae on endopod of 3rd maxilliped	1	0	1
Setae on uropods (exopod & endopod)	12–13, 9–10	13–15, 10–11	13–14, 10–11
Zoea V			
Total length (mm)	3·12–3·63	3·90–4·00	4·82–5·44
Aesthetascs on antennule	3, 1 subterminal	3, 1 subterminal	4, 2 subterminal
Setae on antennal scale	12–13	13–14	14–16
Mandible	with palp	with palp	with palp
Setae on basal endite of maxillule	6 + 3	6 + 4 + 1	6 + 4 + 1
Setae on exopod of maxilla	14–15	13–14	12–14
Setae on endopod of 3rd maxilliped	0	0	0
Setae on uropods (exopod & endopod)	14–15, 10–12	13–15, 10–11	15–18, 14–16

abundant in all stations where the larvae were collected. The presence of the three species is therefore not recorded separately in the Station List.

From the second stage onwards each larval species can be distinguished by the combined characters listed in Table 1. The second species agrees with the larval description of *U. affinis* (Say) given by Sandifer (1973) and this material has been assigned to that species.

Description of the larval stages

The larvae of *Upogebia* sp. A are described in detail. Differences between the three species are observed in the size, the number and position of the antennular aesthetascs, the number of setae on the antennal scale, the presence or absence of a palp bud on the mandible, the number and arrangement of setae on the basal endite of the maxillule, the number of setae on the exopod of the maxilla and the endopod of the third maxilliped and also the number of setae on the uropods. The larvae of *U. affinis* and *Upogebia* sp. B are described with special consideration for these differential characters.

***Upogebia* sp. A**

Zoea I. From station CPOM 421 (18°54.5′N, 91°51′W) where apparently it is the only *Upogebia* sp. present.

c.l. 0·70–0·75 mm
t.l. 1·85–2·00 mm

Carapace (Fig. 1A) longer than broad with long rostral spine. Cervical groove present but very indistinct. Eyes partly fused to anterior margin of carapace.

Antennule (Fig. 1D) unsegmented with 3 aesthetascs and 2 setae distally and 1 subterminal plumose seta.

Antenna (Fig. 1C) exopod with 1 spine and 8–9 setae, endopod stout unsegmented with 3 apical setae, basis with 1 spine.

Mandible symmetrical with ventral part slightly expanded and without a palp.

Maxillule (Fig. 1F) endopod 3-segmented with 2, 2, 4 setae; basal endite with 5 setae placed into 2 rows, the lower with 2, the upper with 3 setae (setal formula of the basal endite can be written as 2 + 3); coxal endite with a single row of 6–7 setae.

Maxilla (Fig. 1E) scaphognathite with 5 marginal setae, endopod unsegmented with 6 setae, bilobed basal and coxal endites with 9–10 and 11–12 setae respectively.

First maxilliped (Fig. 1K) exopod 2-segmented with 4 apical setae, endopod 5-segmented with 3, 2, 1, 2, 5 setae, one seta on last segment being lateral; basis with 11, coxa with 2 setae respectively.

Second maxilliped (Fig. 1L) exopod 2-segmented with 4 apical setae, endopod 4-segmented with 2, 2, 2, 5 setae, 1 lateral seta on the last segment; basis with 2 setae.

Third maxilliped (Fig. 1M) exopod and endopod unsegmented and unarmed.

Pereiopods 1 and 2 (Figs 1G, H) exopods and endopods separated from basis, unsegmented and without setae.

Pereiopod 3 (Fig. 1I) elongated, biramous bud without setae.

Pereiopods 4 and 5 (Figs 1J4, J5) elongated, uniramous buds without setae.

Abdomen (Fig. 1A) 5-segmented, 5th segment with a pair of large lateral spines, 6th segment fused to telson.

Telson (Fig. 1B) roughly triangular with 7 + 7 spines, spine 2 reduced to a hair, anal spine present.

Zoea II. c.l. 0·85–0·90 mm
t.l. 2·35–2·45 mm

Carapace (Fig. 2A) with eyes now free.

Antennule (Fig. 2D) now with an exopod demarcated from the peduncle with 3 aesthetascs and 3–4 setae and an endopod with 1 seta; peduncle with 2 large inner plumose setae and a few outer small ones.

Antenna (Fig. 2E) exopod with 1 spine and 10–11 setae, basis now with 2 spines.

Mandible (Fig. 2C) unchanged.

Maxillule (Fig. 2J) endopod unchanged, basal endite with 7 setae, setal formula 4 + 3; coxal endite with 7 setae.

Maxilla (Fig. 2I) scaphognathite with 6–7 setae, endopod unchanged, basal and coxal endites with 10 and 12 setae respectively.

First maxilliped (Fig. 2F) exopod now with 6 apical setae, endopod 5-segmented with 2, 3, 1, 2, 5 setae, second and last segments each with a lateral plumose seta.

Second maxilliped (Fig. 2G) exopod now with 6 apical setae, basis with 3 setae.

Third maxilliped (Fig. 2H) exopod now 2-segmented with 6 apical setae, endopod small with 1 plumose seta.

Pereiopod 1 (Fig. 2K) exopod now 2-segmented with 6 setae, endopod unsegmented and unarmed.

Pereiopods 2 and 3 (Figs 2L, M) exopods unsegmented, exopod of pereiopod 2 with 0–4 setae, exopod of pereiopod 3 without setae, endopods of both legs unsegmented and unarmed.

Pereiopods 4 and 5 (Figs 2N, O) exopods absent, endopods more elongated than in previous stage, unsegmented and unarmed.

Pleopods 2–5 (Fig. 2A) as small rounded buds.

Telson (Fig. 2B) now has an unarticulated median spine and a spine formula of 8 + 1 + 8, spine 2 reduced to a hair.

ZOEA III. c.l. 1·02–1·10 mm
t.l. 2·56–2·90 mm

Antennule (Fig. 3F) exopod still carrying 3 aesthetascs, one of which is now subterminal; endopod now separated from peduncle with 1 plumose seta, peduncle with 5 inner plumose setae.

Antenna (Fig. 3E) exopod with 1 spine and 11–12 setae, endopod now without setae, peduncle now 2-segmented.

Maxillule (Fig. 3C) endopod unchanged, basal endite with 4 + 3 setae, coxal endite with 8 setae.

Maxilla (Fig. 3D) scaphognathite with 9–10 setae.

First maxilliped (Fig. 3H) second segment of the endopod now with 4 setae one of which is lateral.

Second maxilliped (Fig. 3G) endopod 4-segmented with 2, 3, 3, 6 setae and with 1 lateral seta on the last segment.

Third maxilliped (Fig. 3I) endopod now larger still with 1 seta.

Pereiopods 1 and 2 (Figs 3J, K) exopods of both legs now 2-segmented with 6 apical setae, endopods large, unsegmented and unarmed.

Pereiopod 3 (Fig. 3L) both exopod and endopod unsegmented and unarmed.

Pereiopods 4 and 5, endopods now large.

Pleopods 2–5 (Fig. 3A) fairly large elongated buds on abdominal segments 2–5.

Abdomen (Fig. 3A) 6th abdominal segment now separated from telson with a pair of small dorsal spines on posterior border.

Telson (Fig. 3B) more elongated, setal formula unchanged.

Uropods (Fig. 3B) exopod and endopod not separated from basis, exopod with 10–11 setae, endopod unarmed.

ZOEA IV. c.l. 1·05–1·15 mm
t.l. 2·85–3·00 mm

Antennule (Fig. 4B) peduncle with 5–6 inner plumose setae, exopod with 3 aesthetascs one of which is subterminal.

Antenna (Fig. 4C) exopod with 12–13 setae.

Maxillule (Fig. 4D) basal endite with 9 setae placed in 2 rows, the lower with 6, the upper with 3 setae (setal formula of 6 + 3), coxal endite with 9–10 setae.

Maxilla, scaphognathite with 10–11 setae, endopod unchanged, basal and coxal endites now with 12–13 and 15–16 setae respectively.

First maxilliped (Fig. 3E) exopod with 6–8 setae, endopod unchanged.

Second maxilliped (Fig. 4F) exopod with 6–8 setae, endopod unchanged except for 1 lateral seta now present on second segment.

Third maxilliped (Fig. 4G) endopod unsegmented, large, still with 1 seta.

Pereiopods 1–3 (Figs 4H, I, J) exopods with 6 apical setae, endopods large, unsegmented.

Pereiopods 4 and 5 (Figs 4K, L) endopods large, unsegmented.

Pleopods 2–5 (Fig. 4A) larger than in previous stage.

Uropods (Fig. 4M) exopod and endopod now separated from basis, exopod with 12–13 setae, endopod with 9–10 setae.

Telson (Fig. 4M) approximately rectangular, spine formular unchanged but spine 2 is no longer hair-like, spine 4 largest and continuous with telson.

Zoea v. c.l. 1·19–1·32 mm
t.l. 3·12–3·63 mm

Antennule (Fig. 5G) and *antenna* (Fig. 5F) unchanged.

Mandible (Fig. 5C) with a small rounded palp.

Maxillule (Fig. 5D) unchanged.

Maxilla (Fig. 5E) scaphognathite with 14–15 setae.

First and second maxillipeds (Figs 5I, J) unchanged.

Third maxilliped (Fig. 5H) exopod with 6–8 setae, endopod large, 5-segmented without setae.

Pereiopods 1–5 (Figs 5K–O) all endopods large and 5-segmented.

Pleopods 2–5 (Fig. 5P) uniramous, more elongated than in previous stage but still without a basis.

Uropods (Fig. 5B) exopod with 14–15 setae, endopod with 10–12 setae.

Telson (Fig. 5B) unchanged.

Upogebia affinis (Say)

Zoea i. This stage cannot be distinguished from that of *Upogebia* spp. A or B.

Zoea ii. c.l. 0·90–0·98 mm
t.l. 2·30–2·55 mm

Antennule (Fig. 6D) exopod with 2 terminal aesthetascs and 4–5 small setae.

Antenna (Fig. 6E) exopod with 11–12 setae.

Mandible without a palp.

Maxillule (Fig. 6C) basal endite with 7 setae and a setal formula of 4 + 3.

Maxilla (Fig. 6F) scaphognathite with 7 marginal setae.

First and second maxillipeds (Figs 6G, H) do not differ from those of *Upogebia* sp. A.

Third maxilliped (Fig. 6I) endopod with 2 setae.

Periopod 2 (Fig. 6K) exopod usually unarmed.

Zoea iii. c.l. 1·00–1·12 mm
t.l. 2·80–3·06 mm

Antennule (Fig. 7D) exopod with 3 aesthetascs one of which is subterminal, endopod demarcated from peduncle with 1 or 2 setae, peduncle with 3 distal and 5 inner plumose setae.

Antenna (Fig. 7E) exopod with 1 spine and 11–12 setae, endopod sometimes with 1 seta, peduncle with 2 spines.

Mandible without a palp.

Maxillule (Fig. 7F) basal endite with setal formula 4 + 3.

Maxilla scaphognathite with 11–12 marginal setae.

Third maxilliped (Fig. 7C) endopod with 2 setae.

Uropods (Fig. 7B) with 11–12 setae, endopod unarmed.

ZOEA IV. c.l. 1·15–1·22 mm
t.l. 3·00–3·57 mm

Antennule (Fig. 8C) exopod and endopod unchanged, peduncle with 6–7 inner plumose setae.

Antenna exopod with 13–14 setae, endopod stout without setae.

Mandible (Fig. 8B) now with a rounded palp.

Maxillule (Fig. 8D) setae on basal endite now appear in 3 rows, the lowest with 6, the middle with 3–4 and the upper with 1 seta on the lateral side of the endite (setal formula 6 + 3–4 + 1), coxal endite with 10 setae.

Maxilla scaphognathite with 13–14 marginal setae.

Third maxilliped (Fig. 8E) endopod now unarmed.

Uropods exopod with 13–15 setae, endopod with 10–11 setae.

ZOEA V? c.l. 1·36–1·40 mm
t.l. 3·90–4·00 mm

Two specimens of this stage have been found. They differ from larvae of the previous stage by their larger size (Fig. 8G), their larger third maxilliped (Fig. 8H) and pereiopods (Figs 8I–M) the endopods of all of which are 5-segmented. It is not known whether they constitute a separate stage or are only a further developed stage IV. Sandifer (1973) reported 4 stages in the larvae of *U. affinis* of Virginia plankton while according to M. H. Roberts (see Sandifer, 1973) this species passes through 4 or 5 (usually 4) stages in laboratory rearing.

REMARKS. The material examined agrees in most features with the larvae of *U. affinis* described by Sandifer (1973), except that the antennular exopod of Zoea II has 4–5 instead of 6 setae, the maxilla scaphognathite of Zoea II has 7 marginal setae instead of 6 and that of Zoea III has 11–12 setae instead of 9–10.

Upogebia sp. B

This species differs from the two previous ones by its larger size although stage I cannot be distinguished from that of *Upogebia* sp. A or *U. affinis*.

ZOEA II. c.l. 0·95–1·10 mm
t.l. 2·72–2·80 mm

Antennule (Fig. 9C) exopod with 4 terminal aesthetascs.

Antenna exopod with 10 marginal setae.

Mandible without a palp.

Maxillule endopod 3-segmented with 2, 2, 4 setae, basal endite with 4 + 3 setae, coxal endite with 7 setae.

Maxilla exopod with 6 setae.

Third maxilliped (Fig. 9D) endopod small with 1 or 2 setae.

Pereiopod 1 (Fig. 9E) exopod with 4 setae, endopod fairly small, without setae.

Pereiopod 2 (Fig. 9F) exopod with 0–4 setae.

Pereiopod 3 (Fig. 9G) biramous bud, exopod unarmed.

ZOEA III. c.l. 1·19–1·22 mm
t.l. 3·29–3·40 mm

Antennule (Fig. 9I) exopod with 3 aesthetascs one of which is subterminal, endopod with 2 setae.

Antenna exopod with 13 marginal setae.

Maxillule basal endite with 4 + 3 setae, coxal endite with 8 setae.

Maxilla scaphognathite with 10 setae.

Third maxilliped (Fig. 9J) endopod with 1–2 setae.

Uropods (Fig. 9K) basis not yet differentiated, exopod with 11–12 setae, endopod unarmed.

ZOEA IV. c.l. 1·36–1·40 mm
t.l. 3·40–4·00 mm

Antennule (Fig. 10D) exopod now with 4 stout aesthetascs 2 of which are subterminal.
Antenna exopod with 14–15 setae.
Mandible without a palp.
Maxillule (Fig. 10C) endopod unchanged, basal endite with 6 + 3 setae, coxal endite with 9 setae.
Maxilla scaphognathite with 12–13 setae.
Third maxilliped (Fig. 10E) endopod with 1 seta.
Uropods (Fig. 10B) basis now differentiated, exopod with 13–14 setae, endopod with 10–11 setae.

ZOEA V. c.l. 1·66–1·76 mm
t.l. 4·82–5·44 mm

Antennule (Fig. 10H) exopod still with 4 aesthetascs 2 of which are subterminal.
Antenna exopod with 14–16 setae.
Mandible (Fig. 10G) with a palp.
Maxillule (Fig. 10I) basal endite with 6 + 4 + 1 setae, coxal endite with 10–11 setae.
Maxilla scaphognathite with 12–14 setae.
Third maxilliped (Fig. 10J) endopod 5-segmented, without setae.
Pereiopods 1, 2, 3 (Fig. 10K) exopods with 7, 7 and 6 setae respectively, endopods 5-segmented.
Pereiopods 4, 5 endopods 5-segmented.
Uropods exopod with 15–18 setae, endopod with 14–16 setae.

Discussion

The three Mexican larval species studied closely resemble one another and show many similarities with other *Upogebia* larvae previously described. They nevertheless differ from all but one species by having a pair of large lateral spines on the 5th abdominal segments and a pair of small dorsal spines on the posterior border of the 6th. These spines constitute the main features of interest. They were recorded with certainty for the first time by Sandifer (1973) in *U. affinis* from Virginia although one larval species with lateral spines on the 5th abdominal segment was tentatively assigned to *Upogebia* by Dakin & Colefax (1940). The presence of abdominal spines can be considered as an important distinguishing character separating the 3 present American *Upogebia* species, and possibly also the Australian one described by Dakin & Colefax, (1940), from all the remainder. In order to establish whether these spines are present on other *Upogebia* larvae from other regions of the world, larval material in the collections of the BMNH were examined. This included specimens from widely separated geographical regions as the Great Barrier Reef (BM 1951.2.17.2111–2140), the Red Sea (BM 1951.2.17.2103–2110), Nosy Bé (Madagascar) and the Gulf of Guinea. Lateral spines were not found on the 5th abdominal segment of any of these specimens but larvae from the Great Barrier Reef, the Red Sea and Nosy Bé have a small median spine on the posterior border of the 6th abdominal segment from stage III onwards (see Figs 11A, B). In the material from the Gulf of Guinea which includes two or more species, the median spine is present in some larvae and absent in others. Therefore, with respect to the presence of abdominal spines, *Upogebia* larvae do not constitute a zoogeographical homogenous group whilst the absence of lateral spines from the abdomen can no longer be taken as a character holding good for all of them.

Gurney (1938) suggested that the Laomediidae and Upogebiidae are related. As discussed later in this work, one group of laomediid larvae assigned to *Axianassa* sp. and its relatives, have features that link these two families, whilst the presence of a pair of lateral spines on the 5th abdominal segment place them near the Mexican *Upogebia* material described above.

To discover if the grouping of the larvae suggested above also holds good for the adults, and to evaluate the relationship of the genus *Upogebia* with the Laomediidae, adults of the following species of *Upogebia* were examined in the collections of the BMNH.

Species	Origin of the material
U. acutispina de Saint Laurent & Ngoc-Ho	Holothuria Bank, Australia
U. affinis (Say)	S. Carolina, Georgia, USA
U. africana Ortmann	South Africa
U. brasiliensis Holthuis	British Guiana
U. carinicauda (Stimpson)	Thursday Island
	Gulf of Siam
	Madagascar
U. danai (Miers)	Cape Campbell, N. Zealand
U. darwini (Miers)	Phuket, Thailand
	Singapore
	Port Darwin
U. deltaura (Leach)	Plymouth, Britain
	Galway, Ireland
U. giralia Poore & Griffin	Australia
U. hirtifrons (White)	South Seas (Antarctic)
U. issaeffi (Balss)	Tsur Island, Japan
U. lincolni Ngoc-Ho	Java, Indonesia
U. littoralis (Risso)	Napoli, Italy
	Malta
U. major de Haan	Japan
U. miyakei Sakai	Japan
U. omissa Correa	Brazil
U. pugettensis (Dana)	California, USA
U. savignyi (Strahl)	Red Sea
U. simsoni (Thomson)	Australia
U. spinigera (Smith)	Ecuador
	Peru
U. stellata (Montagu)	Plymouth, Britain
	Galway, Ireland
Upogebia sp.	North Kenya
U. talismani Bouvier	Ivory Coast, Africa

The following species were also considered as their descriptions and illustrations (Bozic & de Saint Laurent, 1972; Le Loeuff & Intes, 1974; de Saint Laurent & Ngoc-Ho, 1979) are adequate for comparison (except for the branchial structure of all but one of them, which has been completed by examination of the material deposited at the Museum national d'Histoire naturelle, Paris):

U. aristata Le Loeuff & Intes	Ivory Coast, Africa
U. contigua Bozic & de St Laurent	Gulf of Guinea
U. crosnieri Le Loeuff & Intes	Ivory Coast, Africa
U. furcata (Aurivillius)	Ivory Coast, Africa
U. nitida (A. Milne-Edw.)	Ivory Coast, Africa
U. poensis de St Laurent & Ngoc-Ho	Fernando Po, Gulf of Guinea

Variations in the adult material of *Upogebia* examined concern the presence or absence of an epipod on the maxillipeds, of a large dorsal tooth on the mandible and also the form of the arthrobranchs. Taking *U. issaeffi* as an example, all its 3 maxillipeds (Figs 11D, E, F) have each an exopod, an epipod on the coxa and the 2nd maxilliped to the 4th pereiopod has a pair of arthrobranchs. Its branchial formula can be written as follows:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	–	–	–	–	–
Arthrobranchs	–	2	2	2	2	2	2	–
Podobranchs	–	–	–	–	–	–	–	–
Epipods	1	1	1	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

In *U. issaeffi* as well as in all other *Upogebia* species, an epipod is always present on the 2nd maxilliped.

In *U. issaeffi*, the arthrobranchs consist of a fairly large and flattened structure on either side of the rachis (Fig. 12A) and are referrred to as arthrobranchs type A. The mandible (Fig. 11C) is devoid of a dorsal tooth. In some other species, such as *U. savignyi,* epipods are absent from both the first and the third maxillipeds and arthrobranchs are of type B, with a

Table 2 Various species of *Upogebia* compared according to their epipods, arthrobranchs and other characteristics

Species	Characteristics				
	Epipods on Mxp 1	Mxp 3	Type of arthrobranchs	Dorsal tooth on mandible	Subgeneric division, after de Man
1. *U. affinis*	+	+	A	–	(U)
U. brasiliensis	+	+	A	–	(U)
U. hirtifrons	+	+	A	–	(U)
U. issaeffi	+	+	A	–	(U)
U. major	+	+	A	–	(U)
U. omissa	+	+	A	–	(U)
U. pugettensis	+	+	A	–	(U)
U. spinigera	+	+	A	–	(U)
2. *U. danai*	–	–	A	–	(U)
U. darwini	–	–	A	–	(C)
U. hexaceras	–	–	B	–	(C)
U. savignyi	–	–	B	–	(C)
U. simsoni	–	–	A	–	(U)
Upogebia sp.	–	–	B	–	(C)
3. *U. carinicauda*	+	–	C	–	(U)
U. giralia	+	–	C	–	(U)
4. *U. acutispina*	–	+	B	–	(U)
U. africana	–	+	C	+	(U)
U. aristata	–	+	C	+	(U)
U. contigua	–	+	B	–	(U)
U. crosnieri	–	+	C	+	(C)
U. deltaura	–	+	C	+	(C)
U. furcata	–	+	C	+	(C)
U. lincolni	–	+	C	–	(U)
U. littoralis	–	+	C	+	(U)
U. miyakei	–	+	C	–	(U)
U. nitida	–	+	C	+	(C)
U. poensis	–	+	C	+	(U)
U. stellata	–	+	C	+	(U)
U. talismani	–	+	B	–	(U)

slightly flattened tubular structure on either side of the rachis (Fig. 12B). The mandible has no dorsal tooth. In *U. deltaura,* epipods are present on the second and third maxillipeds but not on the first (Fig. 12G); arthrobranchs are similar to those of *U. stellata* (Fig. 12C), of type C, with 2 small tubular structures on either side of the rachis. The mandible is provided with a large dorsal tooth (Fig. 12F). *U. carinicauda,* on the other hand, has epipods on the first and the second maxillipeds, arthrobranchs of type C and no tooth on the mandible.

Upogebia species considered in this work are separated into groups below according to their epipods, arthrobranchs and mandible characteristics:

(*a*) Presence (+) or absence (—) of epipods on the first and third maxilliped. A minute epipod on the first maxilliped (Fig. 12E) is disregarded.

(*b*) Type of arthrobranchs, A, B or C.

(*c*) Presence (+) or absence (—) of a dorsal tooth on the mandible. When present, this tooth may be small (Fig. 12D) or large (Fig. 12F).

For comparison, the subdivision of *Upogebia* by de Man (1928) into 2 subgenera, *Upogebia (Upogebia)* Leach and *Upogebia (Calliadne)* Strahl is here included. To subgenus *Upogebia* de Man assigned the species with a spine on the antero-lateral margin of the carapace and in which the fixed finger of the cheliped is shorter than the dactylus, while he placed species in which the antero-lateral carapace is absent and the fixed finger is as long as the dactylus into the sub-genus *Calliadne.* Species are here referred to as:

(*d*) Belonging to subgenus *Upogebia* ((U)) or subgenus *Calliadne* ((C)), after de Man.

The foregoing study (Table 2) reveals that:

(*a*) Although the species in groups 1 & 3 can be assigned to de Man's subgenus *Upogebia,* those belonging to groups 2 & 4 are divided between his subgenus *Upogebia* and *Calliadne* and are seen to be associated indifferently with any type of epipod, of arthrobranch or mandible. It would be necessary to examine more material before refuting or substantiating completely the subdivision of the genus *Upogebia* as suggested by de Man, nevertheless, the limited amount of material examined shows that these divisions should not be upheld at present.

(*b*) The American *Upogebia* belong to the first group that contains species with an epipod on both the first and third maxillipeds. As a reduction of the gill formula is generally considered as an advanced character, *Upogebia* species of the first group would be, in this respect, more primitive than the remainder. They are also more similar to the Laomediidae in all known species of which, epipods are present on all maxillipeds. According to Le Loeuff & Intes (1974), the branchial formula is very homogenous in laomediids, and in *Jaxea novae-zealandiae* Wear & Yaldwyn, it is as follows:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Arthrobranchs	2	2	2	2	2	2	2	–
Podobranchs	–	1	1	1	1	1	1	–
Epipods	1	1	1	1	1	1	1	–
Exopods	1	1	1	–	–	–	–	–

On the other hand, the flattened arthrobranch of type A found in species of the first group is similar to that of the Laomediidae (see Wear & Yaldwyn, 1966; Le Loeuff & Intes, 1974) and could be considered as the most primitive of the 3 types. The species of this group possess characters of the subgenus *Upogebia,* and some, such as *U. affinis* and its relatives, produce larvae with a pair of lateral spines on the fifth abdominal segment; these are probably also primitive features. Nevertheless, there is variation in the larval morphology within the same group as abdominal spines are absent from the larvae of *U. pugettensis* (Hart, 1937) and *U. major* (Kurata, 1965).

(*c*) In the second group of species arthrobranchs of type A and B are found. Type B, with a single slightly flattened structure on either side of the rachis, is somewhat similar to type A and suggests the next stage in the evolution of arthrobranchs in *Upogebia* along with the disappearance of the epipods from both the first and the third maxillipeds.

(*d*) In the third and fourth groups of species arthrobranchs of type C are generally found and they probably represent the most evolved type in *Upogebia.* Epipods have now reappeared either on the first or the third maxilliped and a group of African and Mediterranean species, i.e. *U. crosnieri, U. deltaura,* appear to have developed a dorsal tooth on the mandible at this stage of evolution.

(*e*) The above suggestions of evolutionary trends in the Upogebiidae are speculative. They agree with the recent work by de Saint Laurent & Le Loeuff (1979) in the following points: 1. Primitive forms of the family would have a subcheliform pereiopod 1; 2. The presence of an antero-lateral carapace spine is probably another primitive character; 3. There would be a tendancy during evolution towards the disappearance of epipods on the first maxilliped.

However the suggestions presented here disagree with the above mentioned authors who regard arthrobranchs of type A (*'lamelles branchiales larges et entières'*) as the most evolved form and consider that the American group of *Upogebia* as advanced rather than primitive. Besides having arthrobranchs of type A, American species examined in this work are provided with certain characters also considered by de Saint Laurent & Le Loeuff as primitive. These are the presence of an epipod on the first maxilliped, a subcheliform pereiopod 1 and an antero-lateral carapace spine.

(*f*) De Saint Laurent & Le Loeuff (1979) also suggested the grouping of known species of *Upogebia* and discussed the relationship of those of the Atlantic and East Pacific. The conclusions based on the limited amount of material examined here agree in general with this.

B. Larvae of a species of Laomediide attributed to *Axianassa*

Description of the larval stages

Zoea I. c.l. 0·85–0·90 mm
t.l. 2·00–2·10 mm

Carapace (Figs 13A, B) longer than broad with long rostral spine. Cervical groove present but indistinct. Eyes fused to anterior margin of carapace.

Antennule (Fig. 13C) unsegmented with 3 aesthetascs and 2 setae distally and a subterminal plumose seta.

Antenna (Fig. 13D) exopod with 1 spine and 10 setae, endopod stout with 3 apical setae, peduncle with 1 spine.

Mandibles (Fig. 13E) asymmetrical with the left one sickle-shaped. Left lobe of paragnath (Fig. 11L) also sickle-shaped.

Maxillule (Fig. 13F) endopod unsegmented with 3 apical setae, basal and coxal endites each with 4 setae.

Maxilla (Fig. 13G) scaphognathite with 5 setae, endopod small, unsegmented with 2 setae, bilobed basal and coxal endites carrying 8 and 5 setae respectively.

First maxilliped (Fig. 13H) exopod 2-segmented with 4 apical setae, endopod 4-segmented with 1, 1, 2, 5 setae one of which is lateral on last segment; the basis has 4 setae.

Second maxilliped (Fig. 13I) exopod 2-segmented with 4 apical setae, endopod 4-segmented, penultimate and last segment with 2 and 4 setae respectively, coxa and basis unarmed.

Third maxilliped (Fig. 13J) exopod 2-segmented without setae, endopod absent.

First and second pereiopods as small rounded buds.

Abdomen (Figs 13A, B) 5-segmented, 5th segment bearing a pair of large lateral spines, 6th segment fused with telson.

Telson (Fig. 13K) spatuliform, with a median hollow and 7 + 7 spines, spine 2 reduced to a hair.

ZOEA II. c.l. 0·95–1·00 mm
t.l. 2·1–2·2 mm

Carapace (Fig. 14A) with eyes now free from the carapace.

Antennule (Fig. 14D) unchanged.

Antenna (Fig. 14E) exopod with 1 spine and 13 setae, basis with 2 spines.

Maxillule (Fig. 14G) endopod and coxal endite unchanged, basal endite now with 5 setae.

Maxilla (Fig. 14F) scaphognathite with 7 setae.

First maxilliped (Fig. 14I) exopod with 6 apical setae.

Second maxilliped (Fig. 14H) exopod with 6 apical setae, second segment of endopod now with 1 seta.

Third maxilliped (Fig. 14K) exopod now has 4 apical setae.

First pereiopod (Fig. 14L) small with short, unsegmented exopod without setae, endopod absent.

Second pereiopod as a small bud.

Telson spatuliform with 8 + 8 or 8 + 1 + 8 setae, spine 2 reduced to a hair, median spine absent (Fig. 14B) or present and small (Fig. 14C). The two forms of telson (with or without median spine) are observed in specimens which otherwise agree with one another in all respects.

ZOEA III. c.l. 1·2–1·4 mm
t.l. 2·8–3·0 mm

Antennule (Fig. 15D) 2-segmented, terminal segment conical with 2 aesthetascs and 2 setae, peduncle with 3 terminal and 3 lateral setae.

Antenna (Fig. 15C) exopod with 1 spine and 15 setae, endopod with 1 seta.

Maxillule (Fig. 15F) endopod unsegmented with 3 apical setae, basal and coxal endites with 7 and 4 setae respectively.

Maxilla (Fig. 15G) scaphognathite with 9 setae, endopod with 2 setae, bilobed basal and coxal endites with 8 and 5 setae respectively.

First maxilliped (Fig. 15H) unchanged.

Second maxilliped (Fig. 15I) the first segment of the endopod now has 1 seta.

Third maxilliped (Fig. 15J) exopod now with 6 apical setae, endopod still absent.

First pereiopod (Fig. 15K) exopod 2-segmented with 4 apical setae, endopod small, near base of basis.

Second pereiopod (Fig. 15L) small bilobed bud, unsegmented.

Third pereiopod, small rounded bud.

Telson: Two forms of telson are observed: Form A (Fig. 15E) with median spine, spine formula 9 + 1 + 9, spine 2 reduced to a hair, spine 4 the largest and continuous with the telson; form B (Fig. 15B) with or without median spine, spine formula 8 + 1 + 8 or 8 + 0 + 8, spine 2 reduced to a hair, spine 3 the largest and continuous with the telson.

There is some variation in the telson: the median spine is always present in form A but sometimes absent in form B and also the spine placed between the hair-like seta and the largest telson process varies from large to small in A, is absent in B.

Specimens with A or B form of telson do not differ in any other respects.

Uropods (Fig. 15C) exopod with 10–12 setae, endopod with 2–3 setae, basis not yet differentiated.

ZOEA IV. c.l. 1·2–1·4 mm
t.l. 2·8–3·0 mm

Carapace (Fig. 16A) now with rostral spine slightly curving upwards.

Antennule (Fig. 16G) with exopod and endopod demarcated from peduncle, exopod fairly large with 2 aesthetascs and 3 setae, endopod small, rounded with 1 small seta, peduncle with 5 terminal setae and 4 lateral ones.

Antenna (Fig. 16H) exopod with 1 spine and 15 setae, endopod with 1 seta.

Mandibles (Fig. 16J) with more teeth on cutting surfaces.

Maxillule (Fig. 16B) endopod with 3 setae, basal and coxal endites with 8 and 4 setae respectively.

Maxilla (Fig. 16C) scaphognathite with 11 setae, endopod small with 2 setae, basal and coxal endites with 10 and 5 setae respectively.

Second maxilliped (Fig. 16F) terminal segment of endopod now with a small lateral seta.

Third maxilliped (Fig. 16K) exopod 2-segmented with 4 terminal setae, endopod very small, rounded, placed near the base of basis.

First pereiopod (Fig. 16M) exopod with 6 apical setae, endopod larger than in previous stage.

Second pereiopod (Fig. 16I) exopod 2-segmented with 4 apical setae, endopod small, placed near base of basis.

Third and fourth pereiopods (Fig. 16L) small bilobed buds.

Fifth pereiopod (Fig. 16L) small rounded bud.

Pleopods, small rounded buds on abdominal segments 2–5.

Telson (Figs 16D, E) two forms of telson are observed both with a median spine: form A with spine formula 10 + 1 + 10, spine 2 hair-like, spine 4 the largest and continuous with the telson, form B with spine formula 9 + 1 + 9, spine 2 hair-like, spine 3 the largest.

Uropods (Fig. 16E) exopod with 1 spine and 14 setae, endopod with 6 setae, basis now differentiated, small.

LAST ZOEA. c.l. 2·1 mm
t.l. 4·5 mm

Only one specimen of this stage is found. There are probably 1 or 2 stages between this one and stage 4 previously described.

Carapace (Figs. 17A, B) with rostral spine curving upwards. Cervical groove present, still indistinct.

Antennule (Fig. 17D) exopod elongated with 1 terminal seta and with aesthetascs divided into groups of 1, 2 and 2; endopod small with 2 setae, peduncle slender with 3 distal setae near the base of the endopod and 8–9 lateral setae.

Antenna (Fig. 17C) exopod with 1 spine and 23–24 setae, endopod stout without setae, peduncle with 2 spines.

Mandibles (Fig. 16N) with more teeth and spines on cutting surfaces.

Maxillule (Fig. 17I) endopod with 3 apical setae, basal and coxal endites with 11 and 5 setae respectively.

Maxilla (Fig. 17H) scaphognathite with 26 setae, endopod small with 2 setae, basal and coxal endites with 10 and 7 setae respectively.

First maxilliped (Fig. 17E) exopod 2-segmented with 6 terminal setae, endopod 4-segmented with 1, 1, 2, 4 setae, the internal lateral seta has been lost, basis with 4 setae.

Second maxilliped (Fig. 17F) exopod 2-segmented with 6 terminal setae, endopod 4-segmented with 1, 1, 2, 4 setae, the internal lateral seta has been lost, basis unarmed.

Second maxilliped to fourth pereiopod each with a pair of epipods.

Third maxilliped (Fig. 17G) exopod 2-segmented with 6 terminal setae, endopod now well developed, elongated, placed near the base of basis, basis unarmed.

First pereiopod (Fig. 17K) exopod 2-segmented with 6 terminal setae, endopod well developed, 5-segmented, cheliform, unarmed, placed near base of basis which is also unarmed.

Second and third pereiopods (Figs 17J, M) exopods 2-segmented with 6 apical setae, endopods 5-segmented, unarmed, placed near the base of basis, basis also unarmed.

Fourth pereiopod (Fig. 17L) exopod 2-segmented, endopod 5-segmented, both unarmed, endopod placed near base of basis, basis unarmed.

Fifth pereiopod (Fig. 17N) exopod absent, endopod 5-segmented, both endopod and basis unarmed.

Second to fifth pleopods (Fig. 16O) exopods and endopods lanceolate, unarmed, endopods each with a small internal lateral bud.

Uropod (Fig. 17O) exopod with a small spine and 19 setae, endopod with 17 setae, basis well differentiated.

Telson (Fig. 17O) nearly rectangular in shape with posterior base slightly broader than anterior, spine formula 9 + 1 + 9, spine 2 the largest and continuous with the telson, hair-like seta lost.

Discussion

The affinities of the *Axianassa* sp. larvae described above to some other Thalassinids are discussed below under 3 headings.

1. The affinities to Menon's Madras larvae

There are many similarities between the present *Axianassa* sp. and the larvae from the Madras plankton described by Menon (1933) as belonging to the Upogebiinae. These are:

(*a*) The general body form and rostrum.

(*b*) Presence of a pair of lateral spines on the 5th abdominal segment and absence of spines or hooks on any others.

(*c*) The shape of the telson and appendages in all larval stages.

(*d*) The first pair of pereiopods is cheliform in the late larval stages.

(*e*) Presence of epipods on maxillipeds 2, 3 and pereiopods 1–4 in the late larval stages.

(*f*) As a small bud is present on the endopod of the pleopods in the last stage of the Mexican species, the postlarvae probably have an *appendix interna* on the pleopods as in Menon's material.

The differences between the two species are as follows:

(*a*) In Menon's material the median spine on the telson does not appear until stage 5 whilst in the Mexican species it is present from stage 2. Nevertheless, its presence varies, as in the same stage it may be missing in some specimens.

(*b*) In stages 3 and 4 the telson of Menon's material resembles the form B of the Mexican species, except for the presence of a median spine. The spinulation of the telson posterior border is the same in both materials. On the contrary, in stage 5 which is considered to be the last in Menon's material, a median spine appears on the posterior border of the telson, and on either side 5 spines are found between it and the largest telson process. In the Mexican larvae there are 7 spines instead.

(*c*) As mentioned by Gurney (1938), Menon's species appears to lack the sickle-shaped left mandible which is present in the Mexican larvae. It is possible that Menon overlooked the left mandible while the right one figured by him is very similar to that of the Mexican species.

(*d*) Menon's material also differs from that of *Axianassa* sp. by not having an exopod on the 4th pereiopod.

It is difficult to know whether the 5th zoea described by Menon is actually the last larval stage of his species. As mentioned above, the Mexican *Axianassa* sp. probably goes through at least 6 or 7 stages before metamorphosis. Its last stage resembles Menon's stage 5 in having all pereiopods well developed and epipods on maxillipeds 2, 3 and pereiopods 1–4. It seems more advanced in having a well developed antennule with aesthetascs divided into groups of 1, 2, 2, a maxilla scaphognathite with more setae and a bare proximal extension. It also has larger pleopods with well differentiated basis and a bud on the endopods, a telson approximating a rectangular shape and more setae on both the exopod and the endopod of the uropods.

As described above, the development of the pereiopods is retarded in *Axianassa* sp. and the 4th leg remains as a bud throughout many stages. Its exopod is probably only differentiated—and yet unarmed—in the last larval stage. This suggests that Menon's species would have to go through more than 5 stages before metamorphosis and that only in its last zoea, would it have developed the exopod of the 4th pereiopod.

On a whole, similarities between Mexican *Axianassa* sp. and Menon's material are evident and they are, with little doubt, closely related. One important feature of this relationship is the presence, in the last stage, of a small bud on all pleopods in the Mexican larvae which would have probably given rise later to an *appendix interna* as observed in the postlarvae of Menon's species. If this is the case these two species could satisfactorily be placed within the same genus; nevertheless, as the exopod on pereiopod 4 is present in one species and apparently absent in the other, this view is a tentative one.

2. The affinities to the Upogebiidae

Can the larvae of *Axianassa* sp. from the gulf of Mexico and also those from Madras described by Menon be identified as upogebiid?

These two species share many common characters with the Upogebiidae which will be discussed later in this work. They differ in the following features:

(*a*) The higher number of larval stages.

(*b*) The shape of the maxillule and maxilla, especially the unsegmented endopod of the former and the very small endopod of the latter.

(*c*) The asymmetrical mandibles the left of which is sickleshaped.

(*d*) The very rudimentary endopod of the third maxilliped.

(*e*) The retarded development of the endopod of the third maxilliped as well as that of all pereiopods.

(*f*) The presence of epipods on maxillipeds 2, 3 and pereiopods 1–4.

(*g*) The presence of an exopod on pereiopod 4 in *Axianassa.*

(*h*) The possible presence of an *appendix interna* on the pleopods in the postlarval stage.

(*i*) The absence of an anal spine.

Gurney (1938), while discussing the position of Menon's larval material from Madras, stated that the presence of epipods on the legs and of an *appendix interna* on the pleopods in the postlarval stage excluded this material from the Upogebiidae. On the other hand, the presence of epipods on legs, of an exopod on leg 4, and especially the presence of the asymmetrical mandibles reveal evidence of a relationship to *Axianassa* sp. with the Laomediidae.

3. The affinities to the Laomediidae

Five genera are known for the adults of the Laomediidae at present. They are: *Laomedia* de Haan, *Naushonia* Kingsley, *Jaxea* Nardo, *Axianassa* Schmitt and *Laurentiella* Le Loeuff & Intes. The larvae have been described for *Laomedia* (Sakai & Miyake, 1964; Yaldwyn & Wear, 1972), *Naushonia* (Gurney, 1938; Gurney & Lebour, 1939; Dakin & Colefax, 1940; Goy & Provenzano, 1978), *Jaxea* (Claus, 1884; Cano, 1891; Bouvier, 1914; Caroli, 1924; Gurney, 1924, 1938; Tattersall, 1938; Dakin & Colefax, 1940; Wear & Yaldwyn, 1966). The first larval stage of *Naushonia crangonoides* Kingsley was collected from plankton and the following 6 stages as well as the first postlarva were obtained from laboratory rearing (Goy & Provenzano, 1978). For the remaining laomediid larvae so far known, descriptions have been based on plankton material.

Mention must be made of the first larval stage of *Laomedia astacina* de Haan described by Sakai & Miyake (1964) and by Yaldwyn & Wear (1972). The larvae described in the former paper are evidently laomediid and it would seem, as Goy & Provenzano (1978) suggested, that the account given by the latter authors are probably of an *Upogebia* species. Nevertheless, *Upogebia* larvae so far known constitute a very homogenous group and those described by Yaldwyn & Wear (1972) differ by the shape of their antennal scale, of their telson and mandibles. The problem can only be settled by new rearing experiments of the species. In the present work, those described by Sakai & Miyake (1964) are considered as the true larvae of *Laomedia astacina.*

Axianassa sp. can be assigned to the Laomediidae as it resembles known larvae of the family as follows:

(*a*) The number of larval stages is 6 or 7.

(*b*) The antennal scale is not segmented, the antennal endopod has 3 apical setae in stage 1.

(*c*) The mandibles are asymmetrical, the left of which is sickle-shaped.

(*d*) The endopod of the maxillule is unsegmented.

(*e*) The endopod of the maxilla is very reduced and the scaphognathite, in late stages, has an proximal extension devoid of setae.

(*f*) Maxillipeds 1 and 2 have the basis long, cylindrical and the setae of the endopods small and delicate.

(*g*) The endopod of maxilliped 3 is rudimentary and placed low on the basis.

(*h*) The development of the endopods of the maxilliped 3 and all pereiopods is retarded.

(*i*) The endopods of the pereiopods remain in most cases unsegmented and inserted low on the basis.

(*j*) There are exopods on pereiopods 1–4, the exopod on pereiopod 4 is often rudimentary and not differentiated until the late stages.

Table 3 Differences between laomediid larvae of the first and the second group

	First group	Second group
Total length (mm) stage 1	*Naushonia* sp.: 2·2 *Jaxea* sp.: 4·5 (Dakin & Colefax, 1940) *Laomedia astacina*: 3·2 (Sakai & Miyake, 1964) *Jaxea novaezealandiae*: 4 (Wear & Yaldwyn, 1966) *Naushonia crangonoides*: 2·6 (Goy & Provenzano, 1978)	Menon's species: 1·8 Gurney species: 2·4 *Axianassa* sp.: 2·1
Total length (mm) Late stages	stage 6: *Naushonia* sp.: 7 *Jaxea* sp.: 15 *J. novaezealandiae*: 13·8–15·2 *N. crangonoides*: 7·8–8·5	Menon's species: 4·25 (stage 5) Gurney's species: 5·7 *Axianassa* sp.: 4·5 (stage 6 or 7)
'Neck' region	more or less elongated	non elongated
Rostrum	curved Exceptions are a species of *Jaxea* (Gurney 1938 : 334) devoid of rostrum and *L. astacina* (Sakai & Miyake, 1964) with an inconspicuous one.	straight, upturned
Antennular peduncle	2-segmented in late stages	unsegmented
Apical spine on antennal scale	absent	present
Procurved pleural hooks on abdominal segments	present at least on segments 2–5 except in a species of *Naushonia* (Gurney, 1938)	present in Gurney's species, absent in others
A pair of lateral spines on abdominal segment 5	absent	present
Appendix interna on pleopods in postlarval stage	presumably absent	presumably present
Median spine on telson in late stages	absent	present
Lateral spines on exopod of uropods in late stages	present in *Jaxea* only	present

(*k*) The telson approximates a triangular shape in stage 1 with a median hollow and a spine formula of 7 + 7, spine 2 is reduced to a hair. There is no median spine.

(*l*) The anal spine is absent.

With the inclusion of the species assigned to *Axianassa* and probably also of Menon's species in the Laomediidae, it is possible to divide the known larvae of this family into 2 groups. To the first group can be assigned all larvae so far described belonging to genera *Laomedia, Naushonia* and *Jaxea.* Into the second are placed the *Axianassa* sp., Menon's species and also a species described by Gurney (1938 : 337) as a laomediid.

Characters separating the two groups are summarized in Table 3.

The most apparent features distinguishing the larvae of the two groups are probably the 'neck' region and the rostrum. This 'neck' region, extending between the mouth and the base of the rostrum, is more or less elongated in the larvae of the first group and normal in the second. On the other hand known larvae of *Jaxea* and *Naushonia* have a small and curved rostrum whilst the three species of the second group have a fairly large one, that is straight and upturned. Two further important differences can be added, (1) the presence or absence of an *appendix interna* on the postlarval pleopods, (2) a median spine on the telson. These features make the separation between the two groups even more distinct. The Mexican larval species here studied can therefore be assigned to neither genera of the first group, i.e. *Laomedia, Jaxea* or *Naushonia.*

Could it belong to genus *Axianassa* or *Laurentiella* the larvae of which are not yet known? The greatest disagreement here is the suggested presence of an *appendix interna* on the pleopods of the post-larvae of the Mexican species that is absent in the known adults of both *Axianassa* and *Laurentiella.* The adult of this Mexican species, although belonging to the Laomediidae, may show important differences from those of *Laomedia, Jaxea* and *Naushonia.* It is possible that the postlarvae possess an *appendix interna* on the pleopods that may disappear in the adult. Nevertheless, as the adults of genus *Axianassa* have been found in the neighbouring area, this material is provisionally identified as *Axianassa* sp. until its adult form is known.

C. The relationships between larvae of the Laomediidae, Upogebiidae and adults of the Glypheidae

With the present knowledge of the larvae of the Laomediidae, certain characters can no longer be considered as holding good for the whole family. These are:

(*a*) The lengthening of the 'neck' region.

(*b*) The pleura of some or all abdominal segments drawn into hooks curved forwards.

(*c*) The absence of a median spine on the telson.

(*d*) The absence of an *appendix interna* on the pleopods.

As discussed above, the larvae of the Laomediidae can be divided into two groups and the above features apply only to the first one. Larvae of the first group have a body shape that clearly distinguishes them from all other thalassinids while those of the second group show a general resemblance to *Upogebia.* The possible relationship between the larvae of the Laomediidae with the adults of the Glypheidae on one hand and with the larvae of the Upogebiidae on the other will be discussed below.

1. Several authors (Burkenroad, 1963; Glaessner, 1969; Forest & de Saint Laurent, 1975) pointed out the relationships between the Glypheidea and the Thalassinidea. The former are a group of crustaceans that flourished in the Jurassic and generally thought to have become extinct by the Eocene but in fact have survived to the Recent. A species, *Neoglyphea inopinata* of the family Glypheidae has been described (Forest & de Saint Laurent, 1975, 1976). The holotype measures 11·5 mm in total length with a triangular curved rostrum, a long epistoma, an elongated area between the mouth and the antennal basis, an *appendix interna* on the pleopods and a suture on the exopod of the uropods. Laomediid larvae of the first group are also provided with a curved rostrum and an elongated 'neck' area and show a resemblance to *Neoglyphea inopinata* in the anterior part of their body; this resemblance is

more pronounced in those belonging to *Naushonia,* the 'neck' region of which is only slightly elongated; postlarve of the second group, on the other hand share with *Neoglyphea* the presence of an *appendix interna* on the pleopods. This perhaps suggests a parental relationship between Glypheidae and Laomediidae and that laomediid larvae show, in their ontogeny, a recapitulation of ancestral characters. It can be noted that adults of the Laomediidae, except *Axianassa,* have a suture either on the exopod or both exopod and endopod of the uropods and those of *Naushonia* (Goy & Provenzano, 1979) have a first pereiopod somewhat similar to that of *Neoglyphea inopinata* (Forest & de Saint Laurent, 1976). Further examination of *N. inopinata* needs to be made to provide information on the above suggestion. Apparently, there are no similarities between its mouth appendages and those of either larval or adult laomediids (de Saint Laurent, personal communication) and its mandibles are symmetrical.

2. Affinities between larvae of the Laomediidae and the Upogebiidae were pointed out by Gurney (1938) who placed both families in an anomuran group with these common characters:

(*a*) Rostrum small and round.
(*b*) Abdomen without dorsal spines.
(*c*) Median spine on telson small or absent, always absent in stage 1.
(*d*) Exopods on leg 3 or legs 3 and 4, never on leg 5.
(*e*) Endopod of maxilliped 3 rudimentary and seated at base of basipod.

In addition, in biramous pereiopods the endopods have also shifted near the base of the basipod.

These above features hold good for all laomediid and upogebiid larvae known at present. Nevertheless, compared with the Upogebiidae, laomediid larvae of the first group differ on account of their lengthened neck area, their long and delicate body, their rostrum and their telson shape. A closer relationship with the Upogebiidae can be found in the second group of laomediid larvae. These, in fact, possess a number of characters which separate them from larvae of the first group and bring them near those of the Upogebiidae. They are listed in Table 3 and summarized below:

(*a*) The non-elongated neck region.
(*b*) The rostrum fairly large, straight and upturned.

It is this shortening of the neck region and the form of the rostrum which contribute mainly to the general resemblance of the second group of the Laomediidae and the Upogebiidae.

(*c*) The unsegmented antennular peduncle.
(*d*) The presence of an apical spine on the antennal scale.
(*e*) The presence of a pair of large lateral spines on abdominal segments 5.

Only a small group of upogebiid larvae, namely *U. affinis* and Mexican *Upogebia* spp. A and B previously described share this character. They probably constitute a group of *Upogebia* larvae the most closely related to the Laomediidae.

(*f*) The presence of a median spine on the telson in the late stages.

In *Axianassa* sp. the median spine appears on the telson in stage 2 as in *Upogebia.* Nevertheless, as described above, there is variation in this respect, that is the median spine can be present or absent in specimens of the same stage.

(*g*) In stage 1 all laomediid larvae have a similar triangular telson shape with a median hollow. Later, the telson in *Axianassa* sp. and other laomediid larvae of the second group has a median spine and a shape definitely approximating that of *Upogebia.*

(*h*) In stage 1 all known laomediid and upogebiid larvae (see Table 3 and Ngoc-Ho, 1977) are rather small with a total length ranging between 2–4 mm. In later stages, while laomediid larvae of the first group reach a much larger size (t.l. 7–15 mm), those of the second group remain small (t.l. 4–6 mm) and resemble the larvae of *Upogebia* (t.l. 3–5 mm).

The last 3 characters mentioned seem to suggest an intermediate position of laomediid larvae of the second group between those of the first and the Upogebiidae. It is interesting to note that while the larvae of *Axianassa* sp. and related species are indisputably laomediid by

the shape and spinulation of their appendages (their mouth appendages especially), they show a general external resemblance to the Upogebiidae by their size, their neck region, their rostrum and telson shape.

Although Gurney (1938) suggested the placing of the Laomediidae and Upogebiidae in the same anomuran group of the Thalassinidea, relationships between adults and larvae of these two families are not at all clear (de Saint Laurent, 1979). The present study of *Axianassa* sp. and its relatives clearly demonstrates that these larvae possess combined characters of both families. However, the postlarvae of the second group of the Laomediidae possibly have an *appendix interna* on the pleopods and this feature separates them from both the Laomediidae of the first group and the Upogebiidae. It is not known whether any relationships exist between them and the Callianassidae or Axiidae, two thalassinid families which also share this character.

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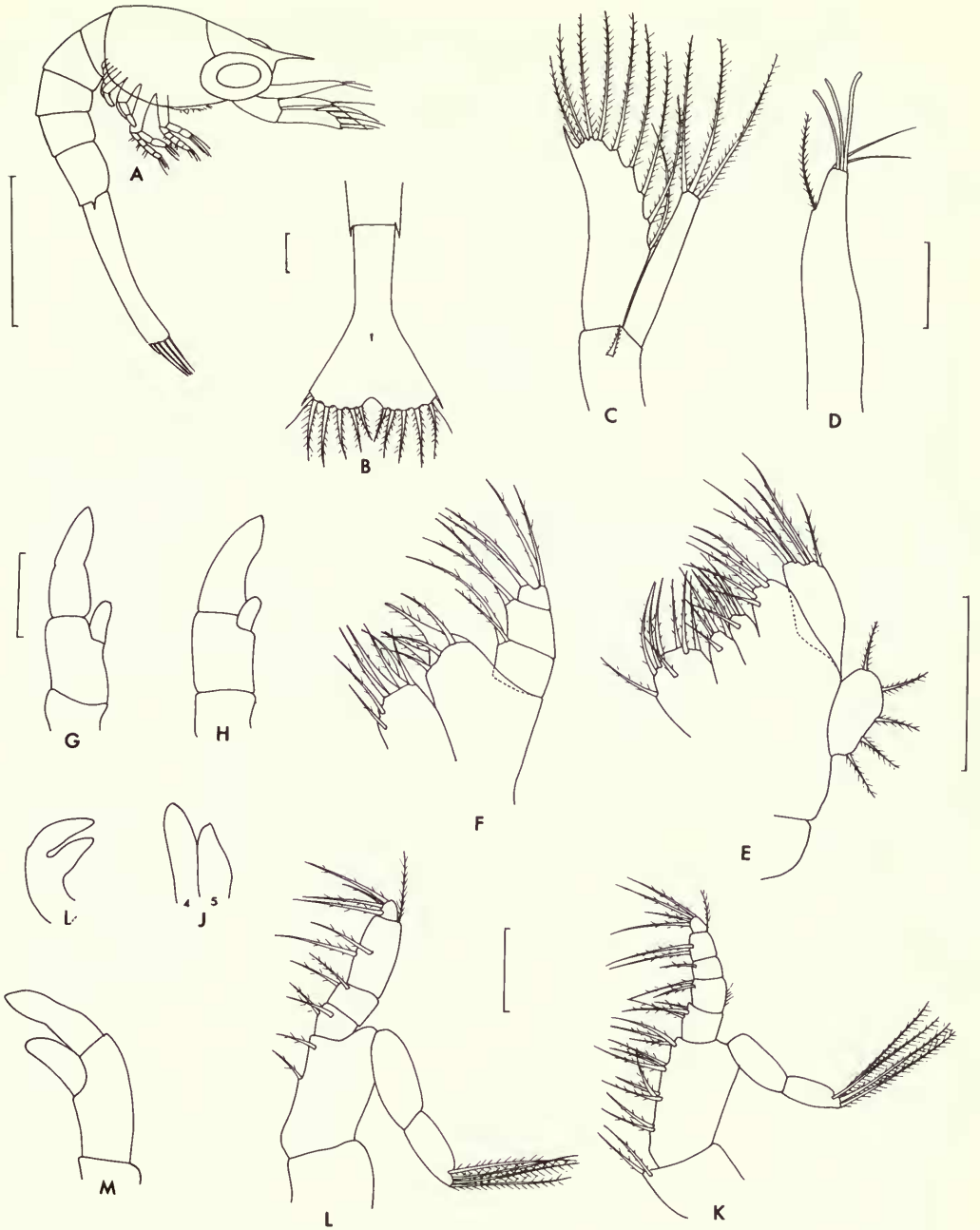

Fig. 1 *Upogebia* sp. A. Zoea I. A, lateral view; B, telson in dorsal view; C, antenna; D, antennule; E, maxilla; F, maxillule; G, pereiopod 1; H, pereiopod 2; I, pereiopod 3; J4 and 5, pereiopods 4 and 5; K, first maxilliped; L, second maxilliped; M, third maxilliped. Scale. 0·5 mm: A; 0·1 mm: B–M.

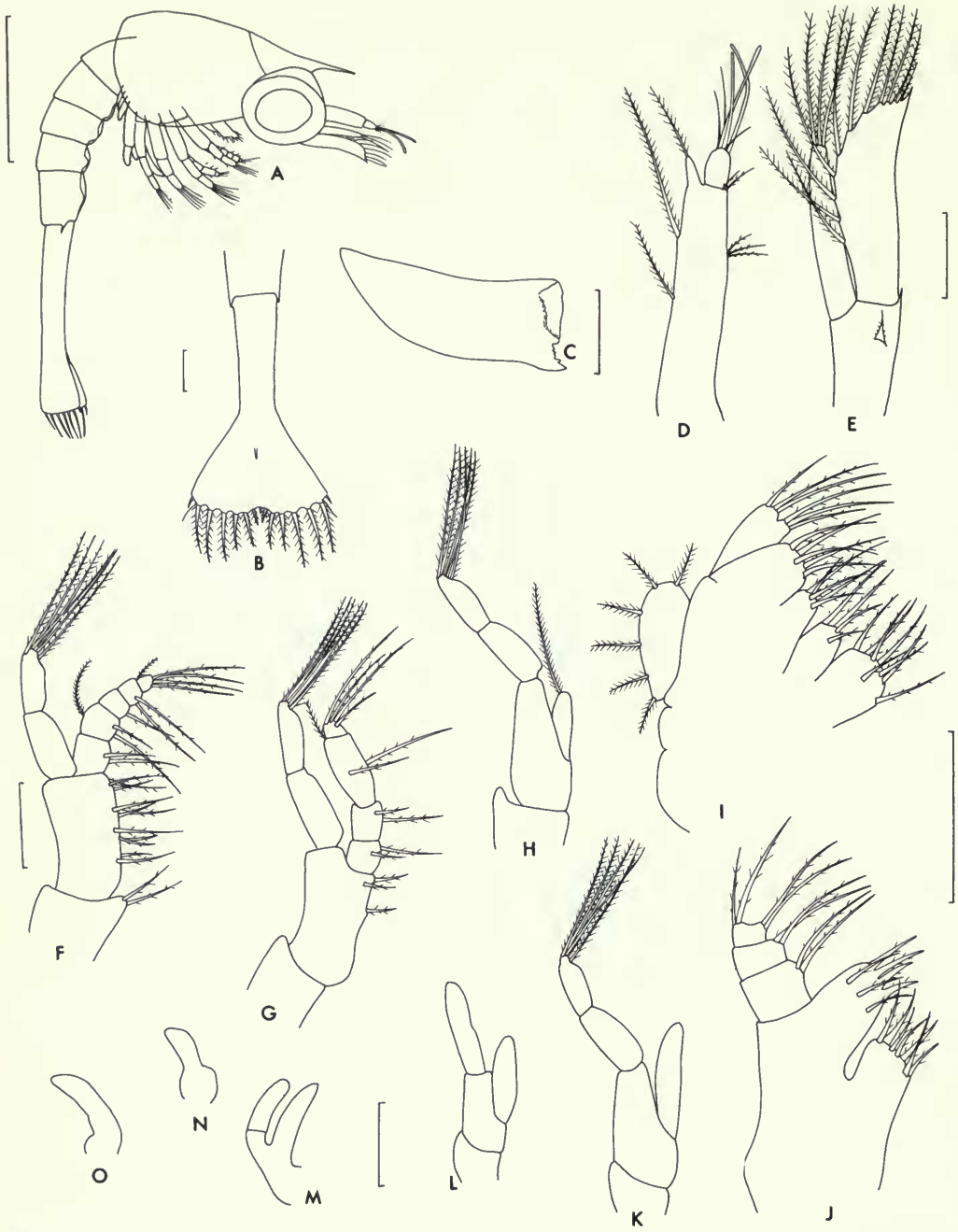

Fig. 2 *Upogebia* sp. A. Zoea II. A, lateral view; B, telson in dorsal view; C, mandible; D, antennule; E, antenna; F, first maxilliped; G, second maxilliped; H, third maxilliped; I, maxilla; J, maxillule; K, L, M, N, O, pereiopods 1, 2, 3, 4, 5 respectively. Scale. 0·5 mm: A; 0·1 mm: B–O.

Fig. 3 *Upogebia* sp. A. Zoea III. A, lateral view; B, telson and uropods in dorsal view; C, maxillule; D, maxilla; E, antenna; F, antennule; G, second maxilliped; H, first maxilliped; I, third maxilliped; J, K, L, pereiopods 1, 2 and 3 respectively. Scale. 0·5 mm: A; 0·1 mm: B–L.

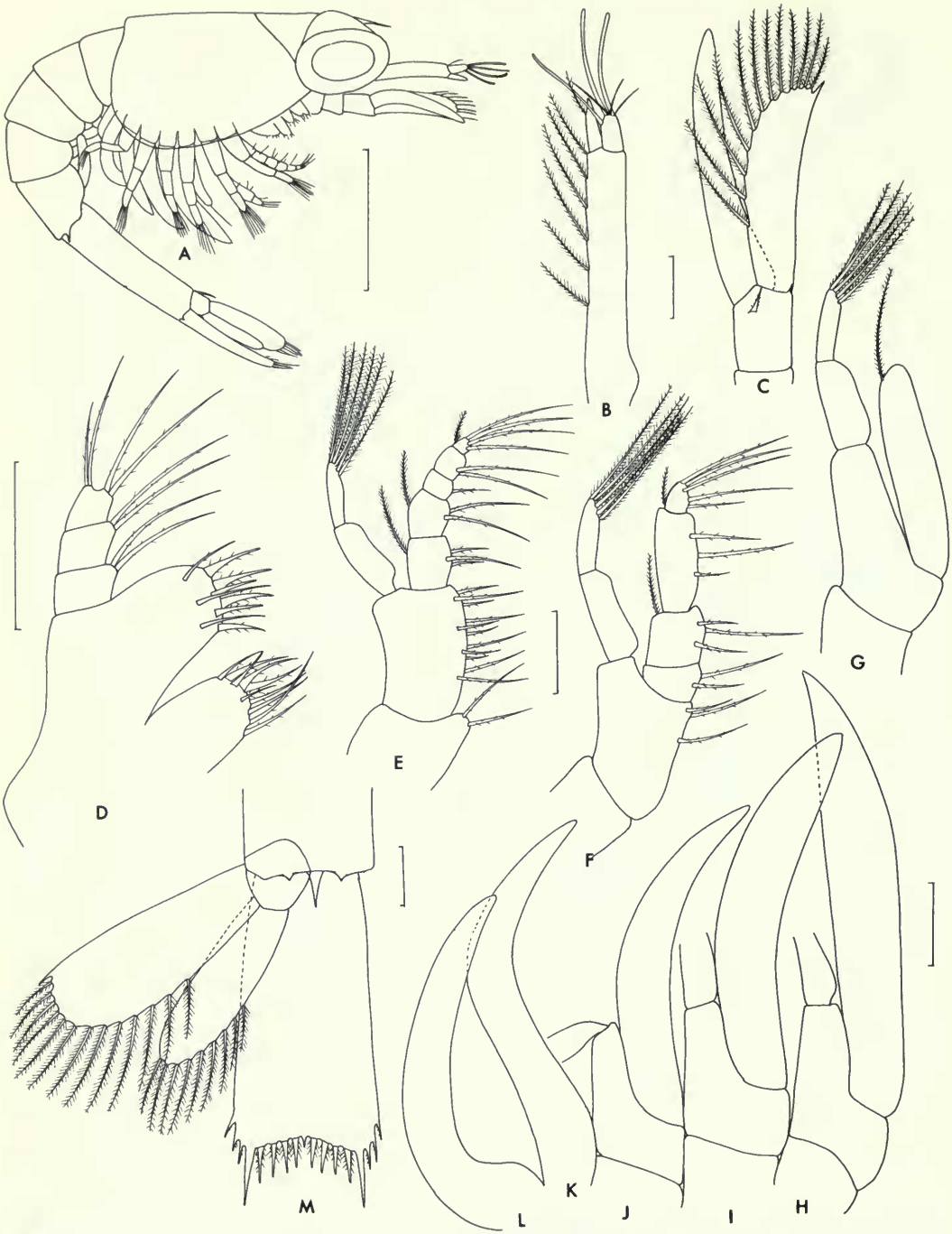

Fig. 4 *Upogebia* sp. A. Zoea IV. A, lateral view; B, antennule; C, antenna; D, maxillule; E, F, G, first, second and third maxillipeds respectively; H, I, J, K, L, pereiopods 1, 2, 3, 4 and 5 respectively; M, telson and uropods in dorsal view. Scale 0·5 mm; A; 0·1 mm: B–M.

Fig. 5 *Upogebia* sp. A. Zoea V. A, lateral view; B, telson and uropods in dorsal view; C, mandible; D, maxillule; E, maxilla; F, antenna; G, antennule; H, third maxilliped; I, first maxilliped; J, second maxilliped; K, L, M, N, O, pereiopods 1, 2, 3, 4 and 5 respectively; P2 and 4, pleopods 2 and 4. Scale. 0·5 mm: A; 0·1 mm: B–P.

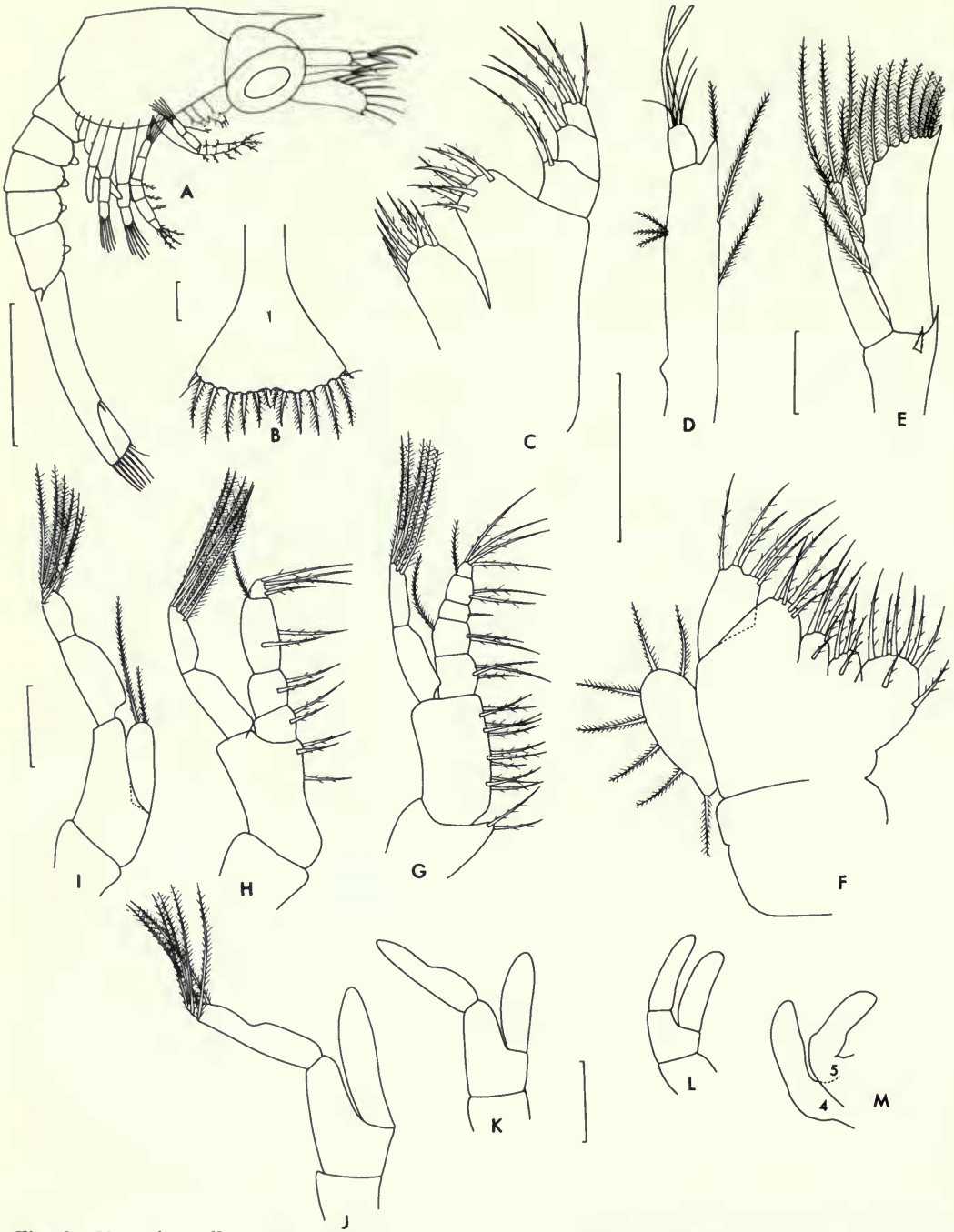

Fig. 6 *Upogebia affinis* (Say). Zoea II. A, lateral view; B, telson in dorsal view; C, maxillule; D, antennule; E, antenna; F, maxilla; G, H, I, first, second and third maxilliped respectively; J, K, L, M4 and M5, pereiopods 1, 2, 3, 4 and 5 respectively. Scale. 0·5 mm: A; 0·1 mm: B–M.

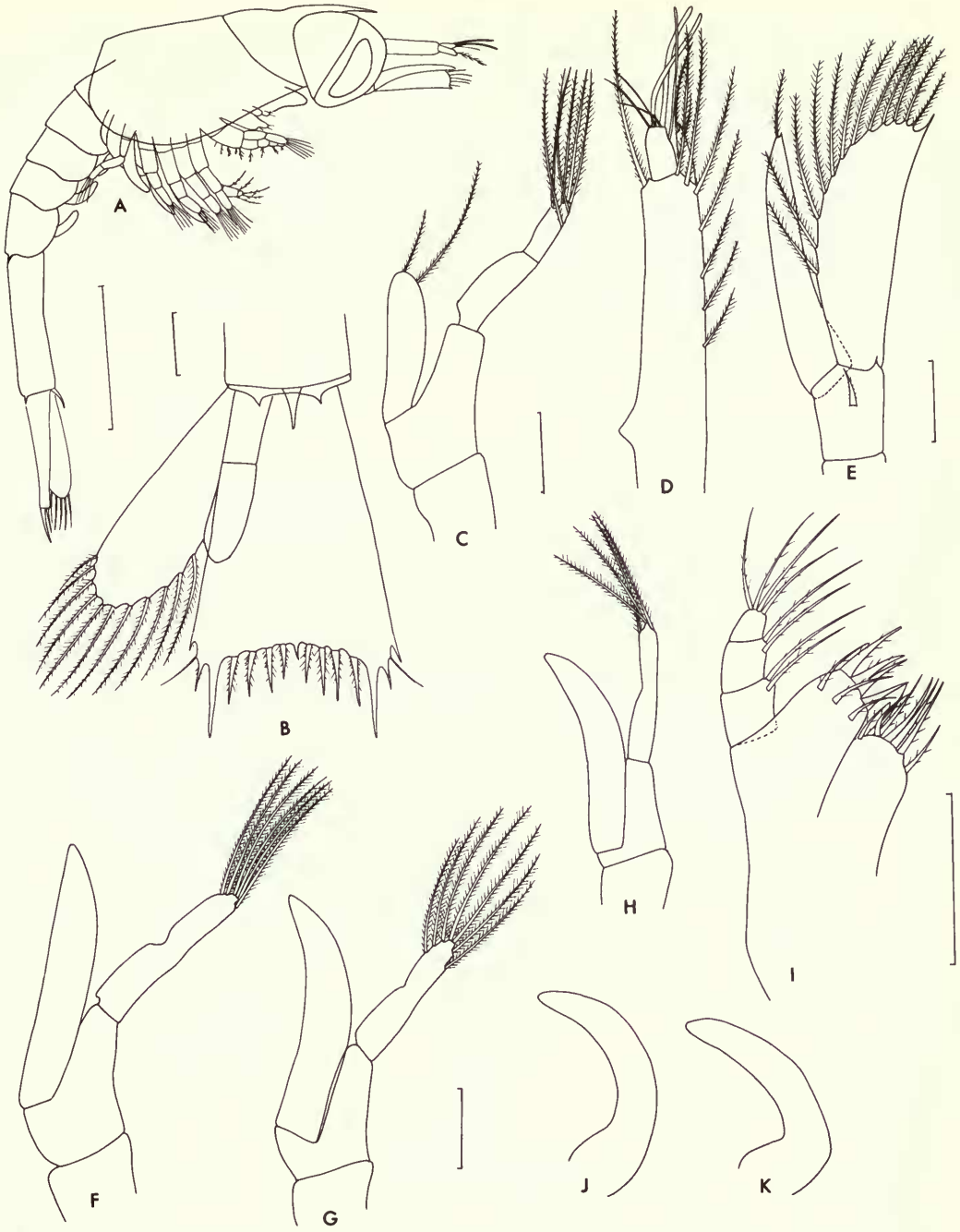

Fig. 7 *Upogebia affinis* (Say). Zoea III. A, lateral view; B, telson and uropods in dorsal view; C, third maxilliped; D, antennule; E, antenna; F, G, H, pereiopods 1, 2 and 3 respectively; I, maxillule; J, K, pereiopods 4 and 5. Scale. 0·5 mm: A; 0·1 mm: B–K.

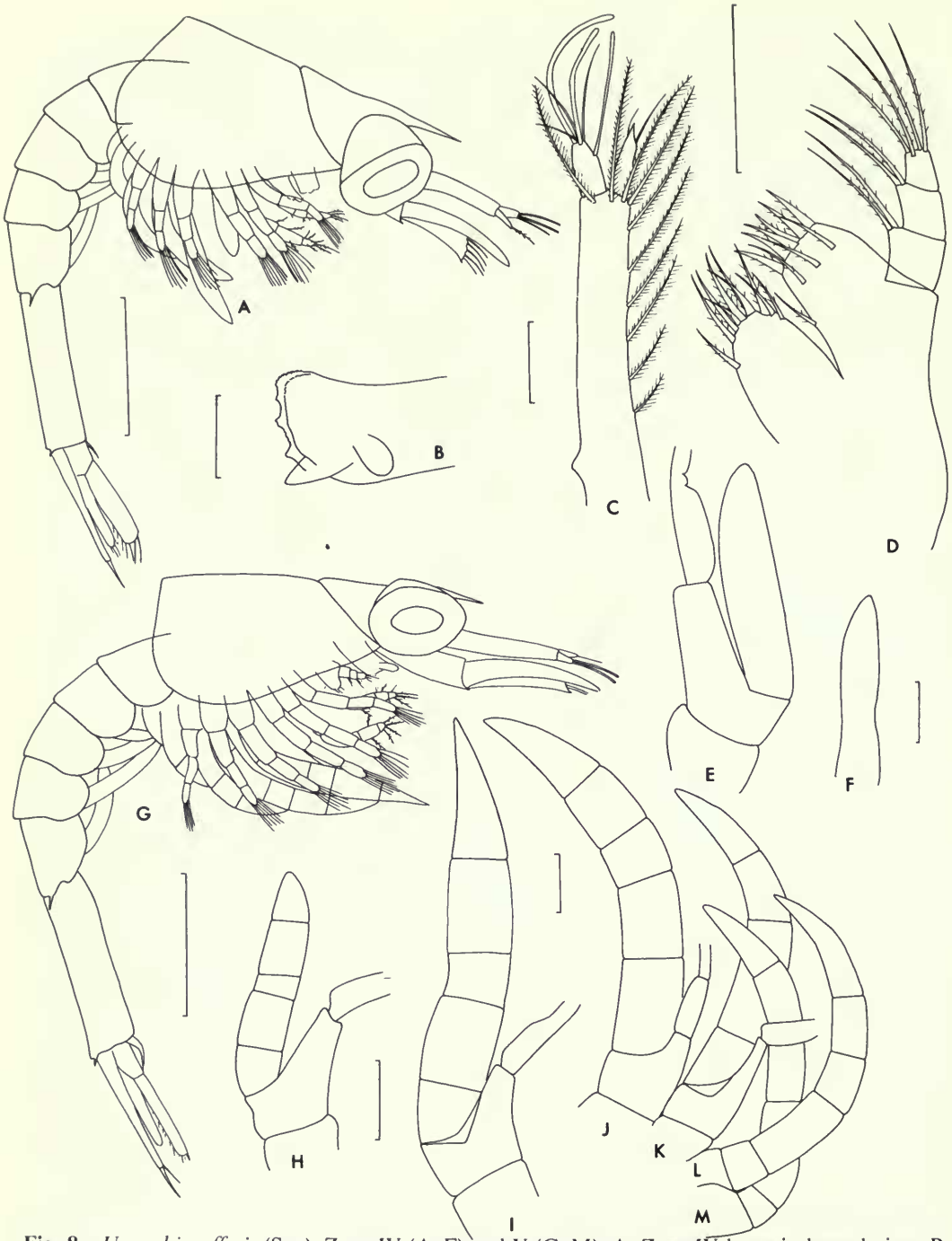

Fig. 8 *Upogebia affinis* (Say). Zoea IV (A–F) and V (G–M). A, Zoea IV larva in lateral view; B, mandible; C, antennule; D, maxillule; E, third maxilliped; F, pleopod 2; G, zoea V larva in lateral view; H, third maxilliped; I, J, K, L, M, pereiopods 1, 2, 3, 4 and 5 respectively. Scale. 0·5 mm: A, G; 0·1 mm: B–F, H–M.

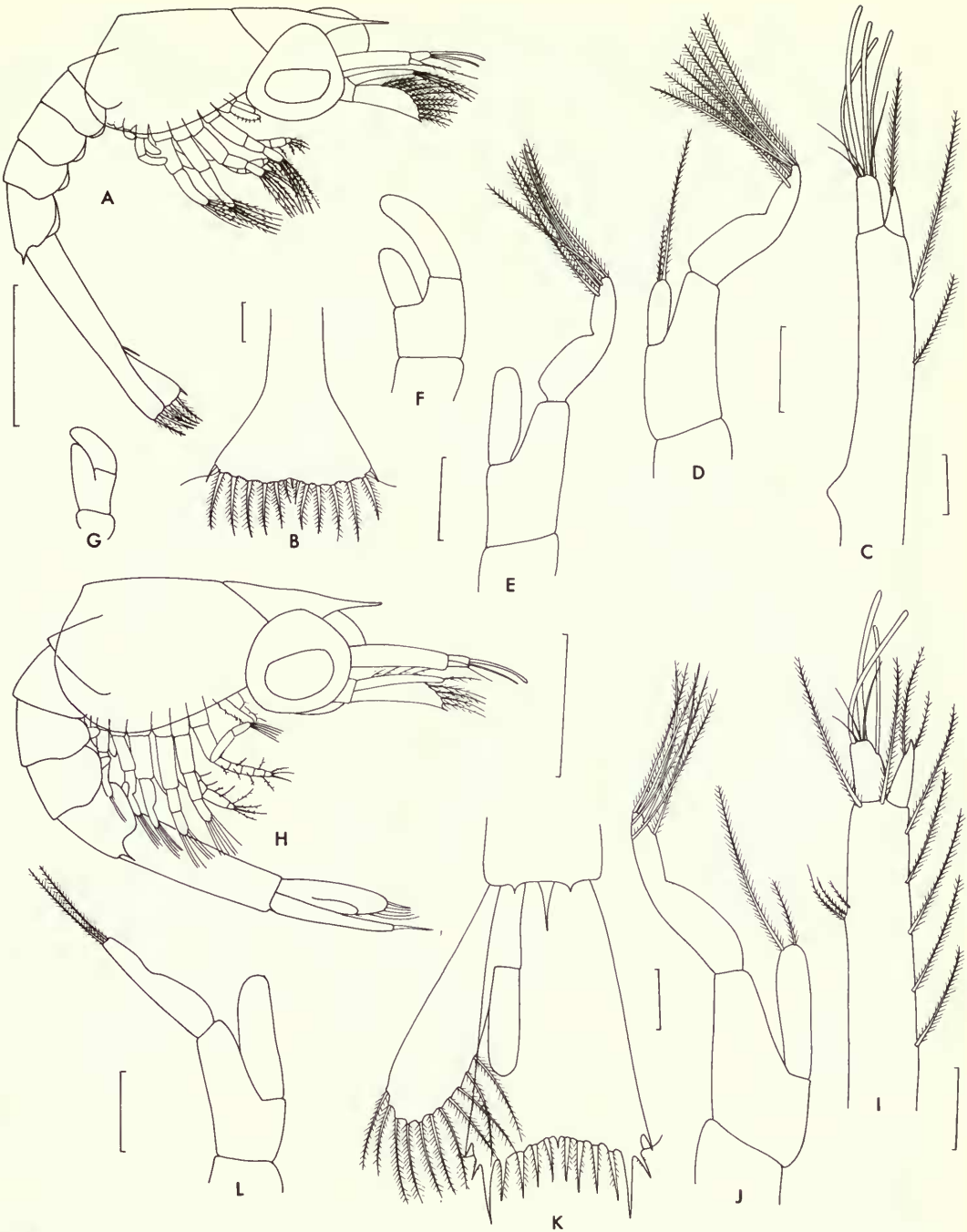

Fig. 9 *Upogebia* sp. B. Zoea II (A–G) and III (H–L). A, zoea II larva in lateral view; B, telson in dorsal view; C, antennule; D, third maxilliped; E, F, G, pereiopods 1, 2 and 3 respectively; H, zoea III larval in lateral view; I, antennule; J, third maxilliped; K, telson and uropods in dorsal view; L, pereiopod 3. Scale. 0·5 mm: A, H; 0·1 mm: B–G, I–L.

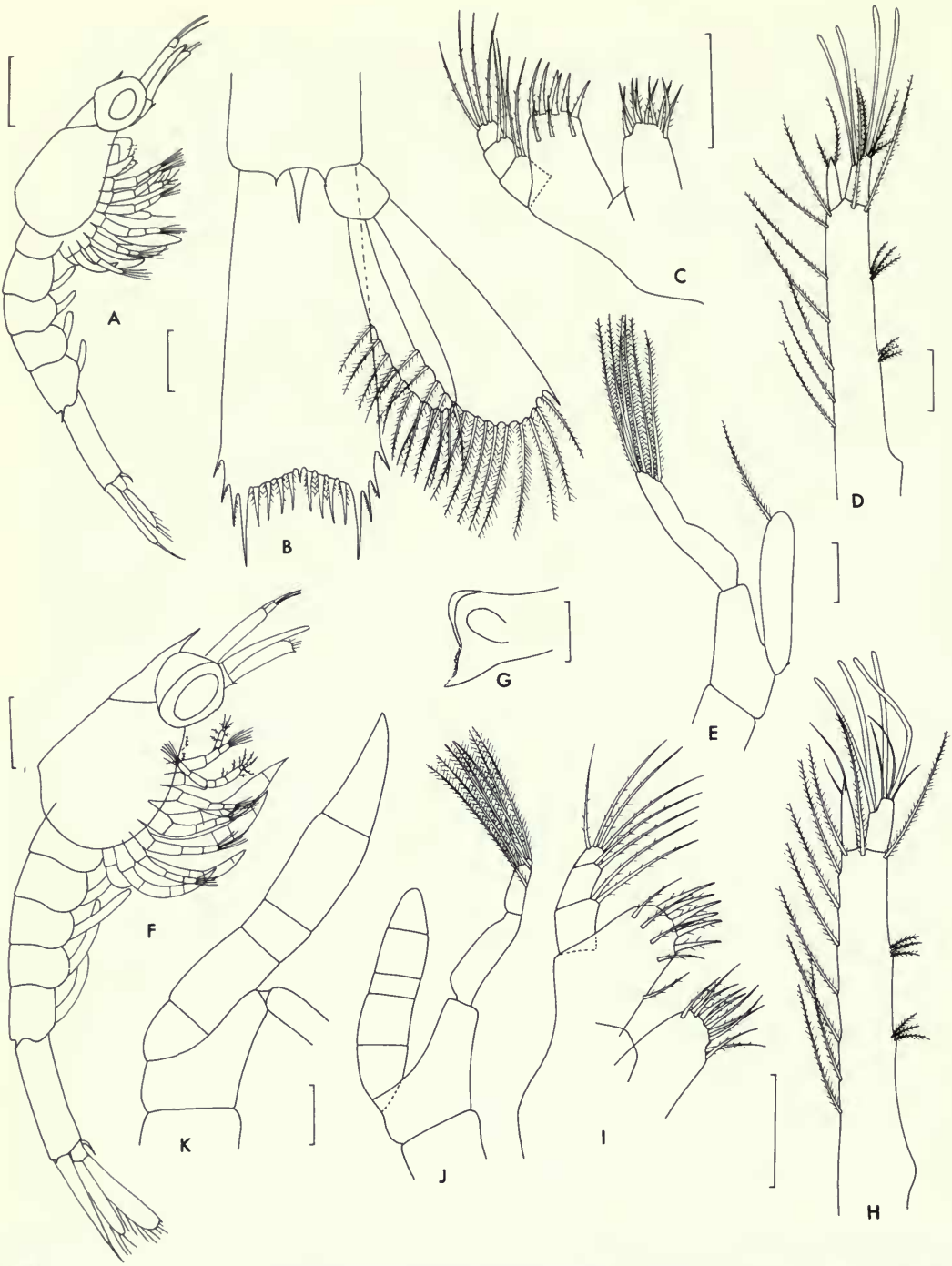

Fig. 10 *Upogebia* sp. B. Zoea IV (A–E) and V (F–K). A, zoea IV larva in lateral view; B, telson and uropods in dorsal view; C, maxillule; D, antennule; E, third maxilliped; F, zoea V larva in lateral view; G, mandible; H, antennule; I, maxillule; J, third maxilliped; K, pereiopod I. Scale. 0·5 mm: A, F; 0·1 mm: B–E, G–K.

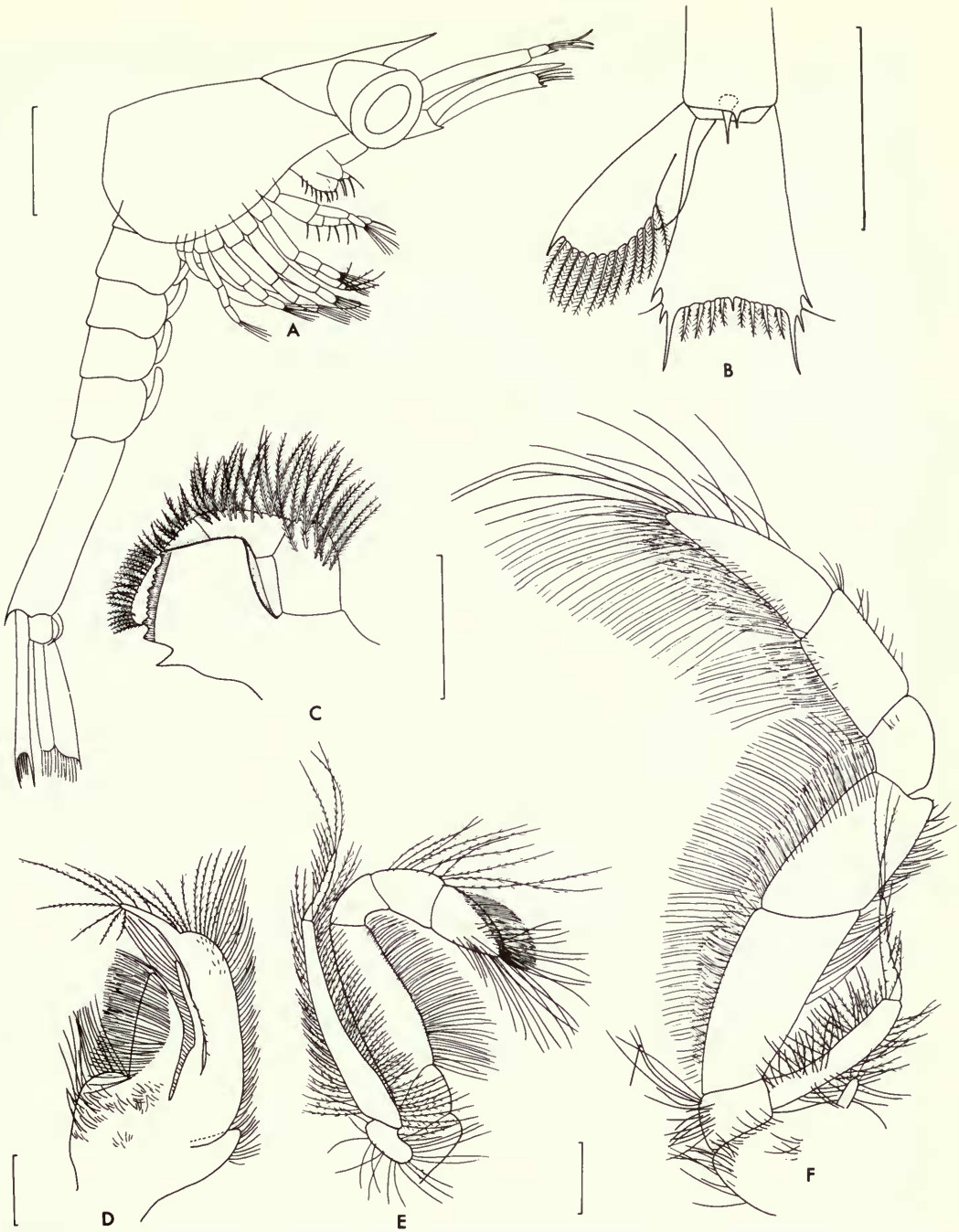

Fig. 11 *Upogebia* larvae and adults. A, B, *Upogebia* sp. larvae from the Great Barrier Reef: A, zoea IV or V in lateral view; B, zoea III, telson and uropods in dorsal view. C–F: *U. issaeffi* adult: C, mandible; D, E, F, first, second and third maxillipeds respectively. Scale. 0·5 mm: A, B; 0·1 mm: C–F.

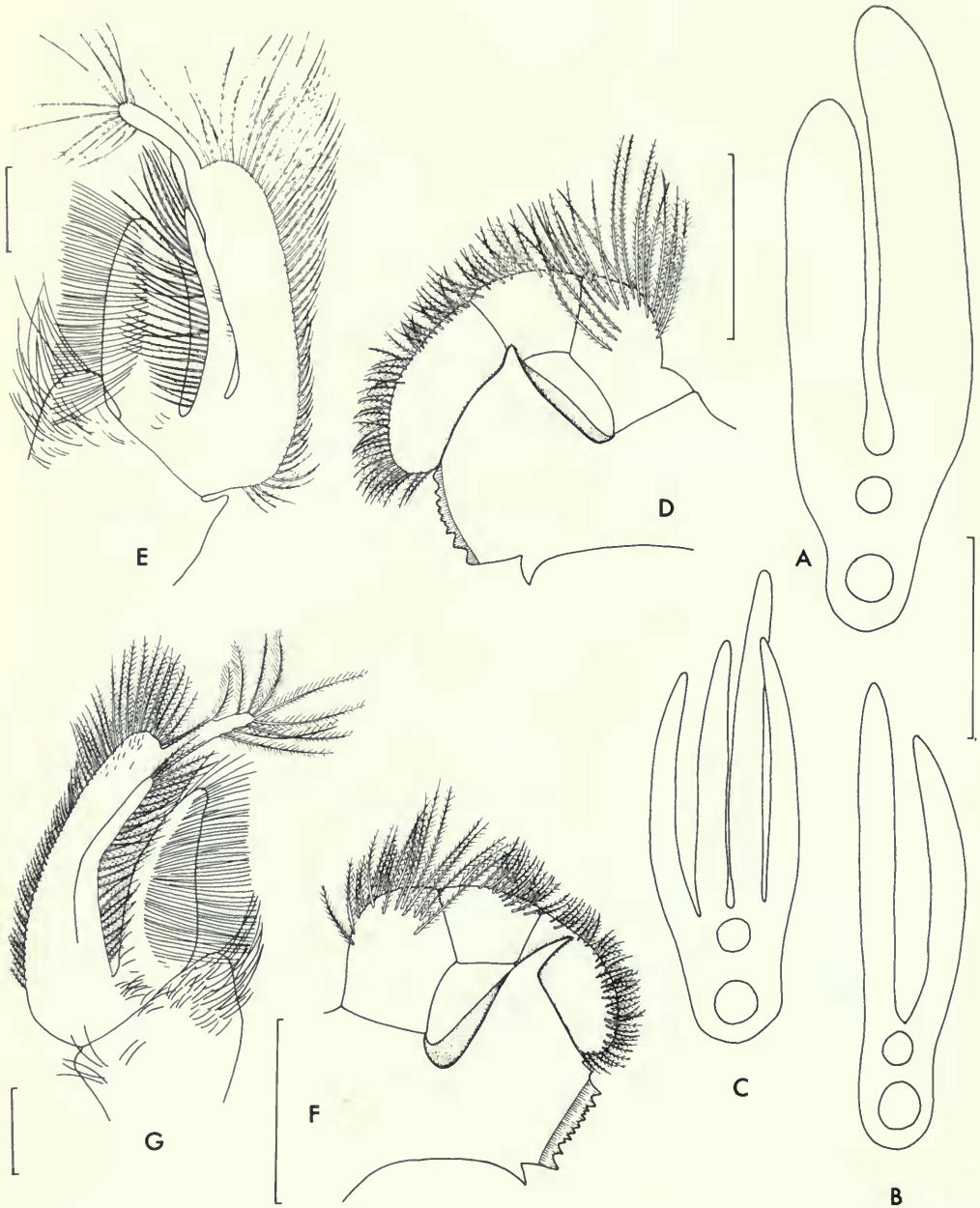

Fig. 12 *Upogebia* adults. A–C: different types of arthrobranchs: A, type A in *U. issaeffi*; B, type B in *U. savignyi*; C, type C in *U. stellata*; D, E, *U. africana*, mandible and first maxilliped; F, G, *U. deltaura*, mandible and first maxilliped. Scale: 1 mm.

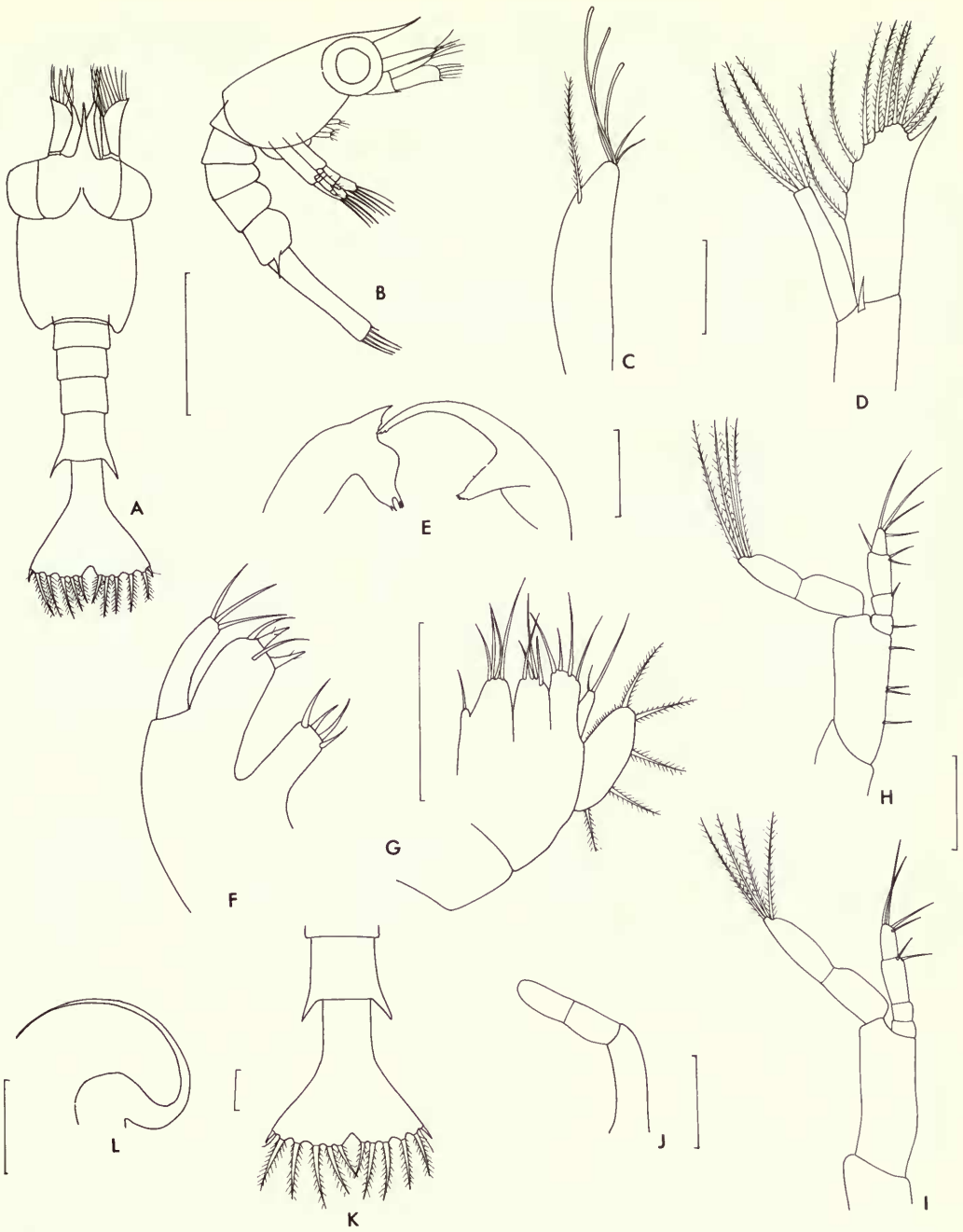

Fig. 13 *Axianassa* sp. Zoea I. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, I, J, first, second and third maxillipeds respectively; K, fifth abdominal segment and telson in dorsal view; L, left lobe of paragnath. Scale. 0·5 mm: A, B; 0·1 mm: C–L.

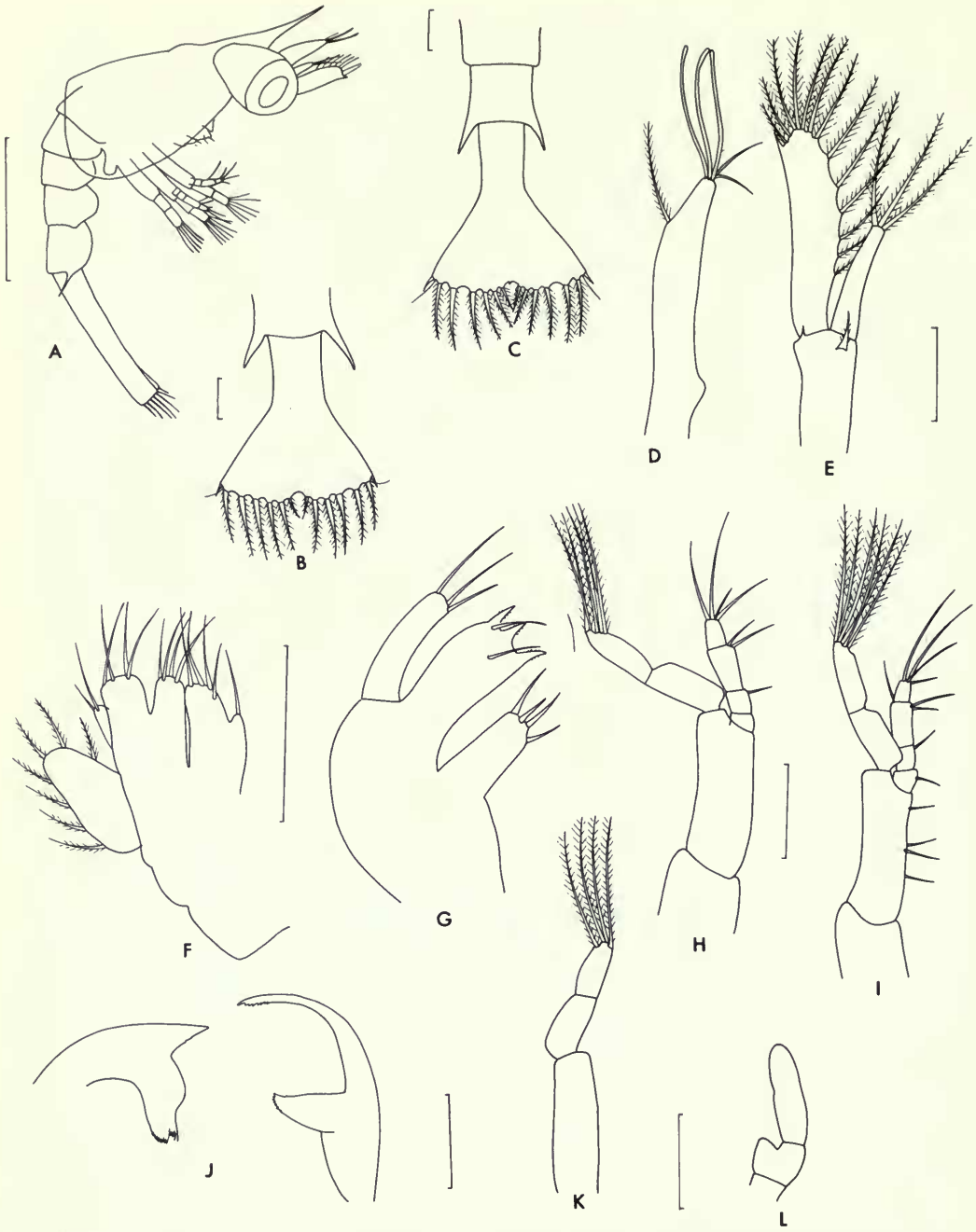

Fig. 14 *Axianassa* sp. Zoea II. A, lateral view; B, telson without median spine in dorsal view; C, telson with median spine in dorsal view; D, antennule; E, antenna; F, maxilla; G, maxillule; H, second maxilliped; I, first maxilliped; J, mandibles; K, third maxilliped; L, first pereiopod. Scale. 0·5 mm: A; 0·1 mm: B–L.

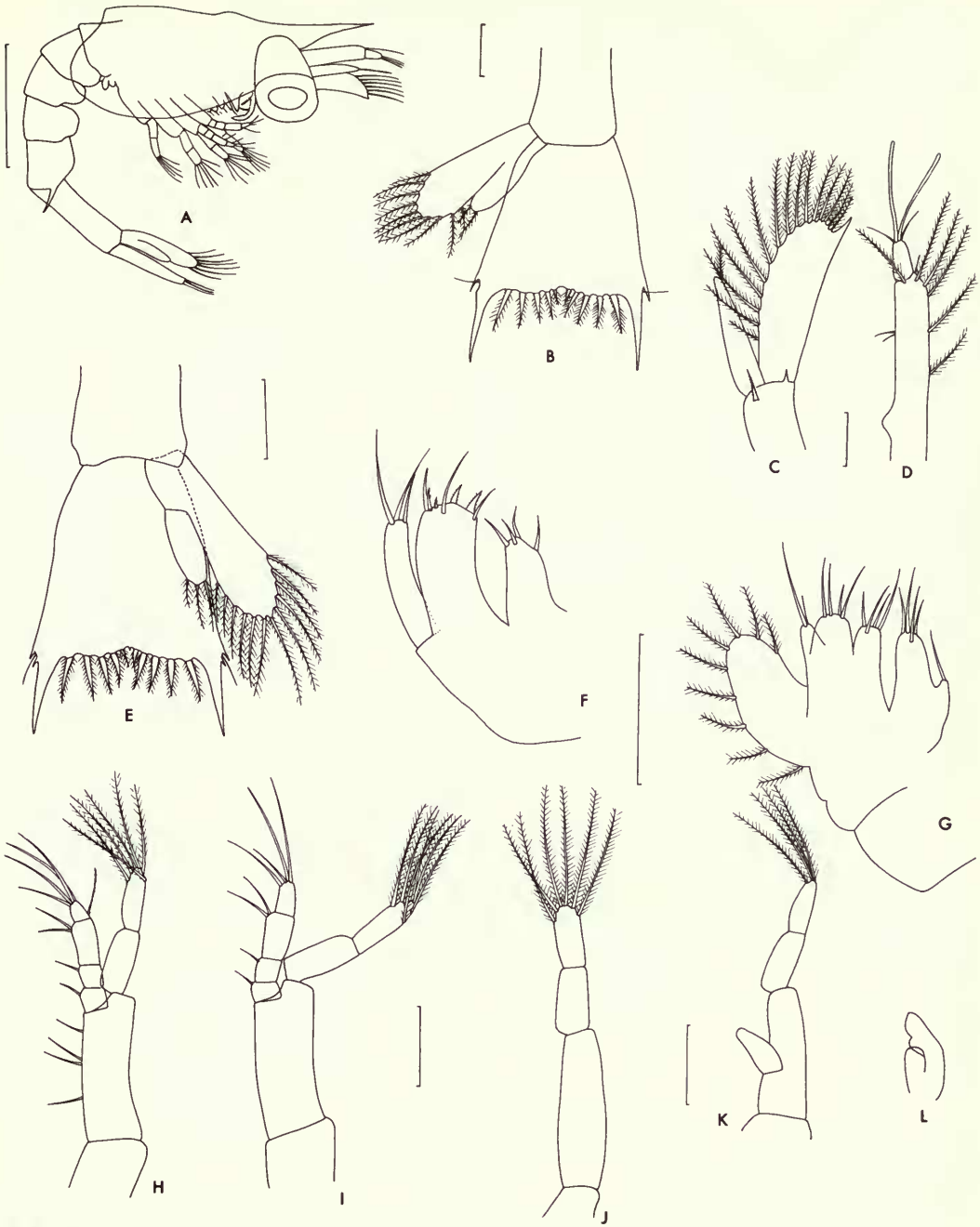

Fig. 15 *Axianassa* sp. Zoea III. A, lateral view; B, telson and uropods of form B in dorsal view; C, antenna; D, antennule; E, telson and uropods of form A in dorsal view; F, maxillule; G, maxilla; H, I, J, first, second and third maxillipeds respectively; K, L, first and second pereiopods. Scale. 0·5 mm: A; 0·1 mm: B–L.

Fig. 16 *Axianassa* sp. Zoea IV (A–M) and last zoea (N, O). A, zoea IV in lateral view; B, maxillule; C, maxilla; D, telson of form B; E, telson of form A and uropods; F, second maxilliped; G, antennule; H, antenna; I, second pereiopod; J, mandibles; K, third maxilliped; L, from right to left, third, fourth and fifth pereiopods; M, first pereiopod; N, O, last zoea, mandibles and second pleopod. Scale. 0·5 mm: A; 0·1 mm: B–O.

Fig. 17 *Axianassa* sp. Last zoea. A, dorsal view; B, lateral view; C, antenna; D, antennule; E, F, G, first, second and third maxillipeds respectively; H, maxilla; I, maxillule; J, second pereiopod; K, first pereiopod; L, fourth pereiopod; M, third pereiopod; N, fifth pereiopod; O, telson and uropods in dorsal view. Scale. 1 mm: A and B; 0·1 mm: C–O.